Chapter 8
Macroevolution and Paleobiogeography of Jurassic-Cretaceous Ammonoids

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8.1 Introduction

Ammonoids of the Jurassic and Cretaceous Periods show remarkable patterns of evolution. While some clades, e.g., Phylloceratina, persist as stable evolutionary lineages throughout this time interval, others experienced incredibly rapid rates of speciation and extinction. The processes responsible for creating this evolutionary volatility have not been clear. While ammonoid extinction rates may reflect heightened sensitivity to environmental conditions, an explanation for their propensity to produce new species and higher taxa has remained elusive. The rich and well-sampled fossil record of ammonoids has enabled paleontologists to document the temporal and spatial context of ammonoid clades in great detail. Synthesizing phylogenetic, temporal, and geographic data may enable us to better understand the patterns and processes of evolution in this extraordinary group of cephalopods.

In this chapter, I briefly review the major clades of Jurassic and Cretaceous (hereafter, J-K) ammonoids, discussing their phylogenetic context and diversity dynamics. Next, I discuss key macroevolutionary processes relevant to understanding the evolutionary volatility of J-K ammonoids. These evolutionary processes are then linked to biogeographic patterns to produce an integrated model for how rapid diversification may occur within ammonoid clades. Throughout the chapter, I highlight topics of current interest that are in need of further study.

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8.2 Phylogeny of Jurassic and Cretaceous Ammonoids

8.2.1 Major Ammonoid Clades

Six ammonoid suborders occurred in the Jurassic-Cretaceous interval: Phylloceratina, Lytoceratina, Ammonitina, Haploceratina, Perisphinctina, and Ancyloceratina. Note that here the traditional suborder "Ammonitina" is split into three suborders (Ammonitina, Haploceratina, Perisphinctina), following Bessenova and Mikhailova (1983, 1991); the term 'Ammonitina *sensu lato'* will be used for all three suborders together. Figure 8.1 shows the stratigraphic and phylogenetic context for the 18 superfamilies within these groups, as currently understood. The evolutionary relationships depicted in Fig. 8.1 are derived from a variety of literature sources, as listed in the figure caption. A comprehensive phylogenetic analysis including all these groups is sorely needed. Several large-scale evolutionary connections remain unclear, including:

a. the origin of Lytoceratina from either Phylloceratina (Arkell et al. 1957; Wiedmann 1969; House 1988) or Psiloceratoidea (Houša 1965; Page 1996, 2008; Guex 1995; Blau et al. 2008; Hoffmann 2010; Guex et al. 2012);
b. derivation of Eoderoceratoidea from either Psiloceratoidea (Schindewolf 1962; Page 1996) or Lytoceratoidea (Donovan et al. 1981; Howarth 2013); note that the latter interpretation makes Ammonitina polyphyletic unless Psiloceratoidea is excluded from it and elevated to suborder status, as suggested by Page (1996, 2008);
c. the origin of Ancycloceratina from Lytoceratina (Arkell et al. 1957; Wiedmann 1966), Spiroceratoidea (Wright et al. 1996), or Perisphinctina (Donovan et al. 1981; Bessenova and Mikhailova 1991; Page 1996; Mikhailova and Baraboshkin 2009);
d. the origin of Turrilitoidea from Lytoceratina (Doguzhaeva and Mikhailova 1981, Bessenova and Mikhailova 1991; Mikhailova and Baraboshkin 2009) or Ancyloceratoidea (House 1988; Wright et al. 1996);
e. derivation of Scaphitoidea from Ancyloceratoidea (Page 1996), Turrilitoidea (Wright 1981), or Perisphinctoidea (Engeser and Keupp 2002).

8.2.2 Biodiversity Through Time

Intensive collection of J-K ammonoids combined with their relatively high preservation potential (Foote and Sepkoski 1999) have allowed paleontologists to document their biodiversity trends through time. Ammonoids show higher evolutionary rates than other mollusks. For instance, Gilinsky (1994, 1998) found that family-level evolutionary volatility (i.e., average net change in diversity per million years) was twice as high for Phylloceratina and four times as high for Ammonitina *sensu lato* as for bivalve mollusks. Yacobucci (2005) calculated per capita origination

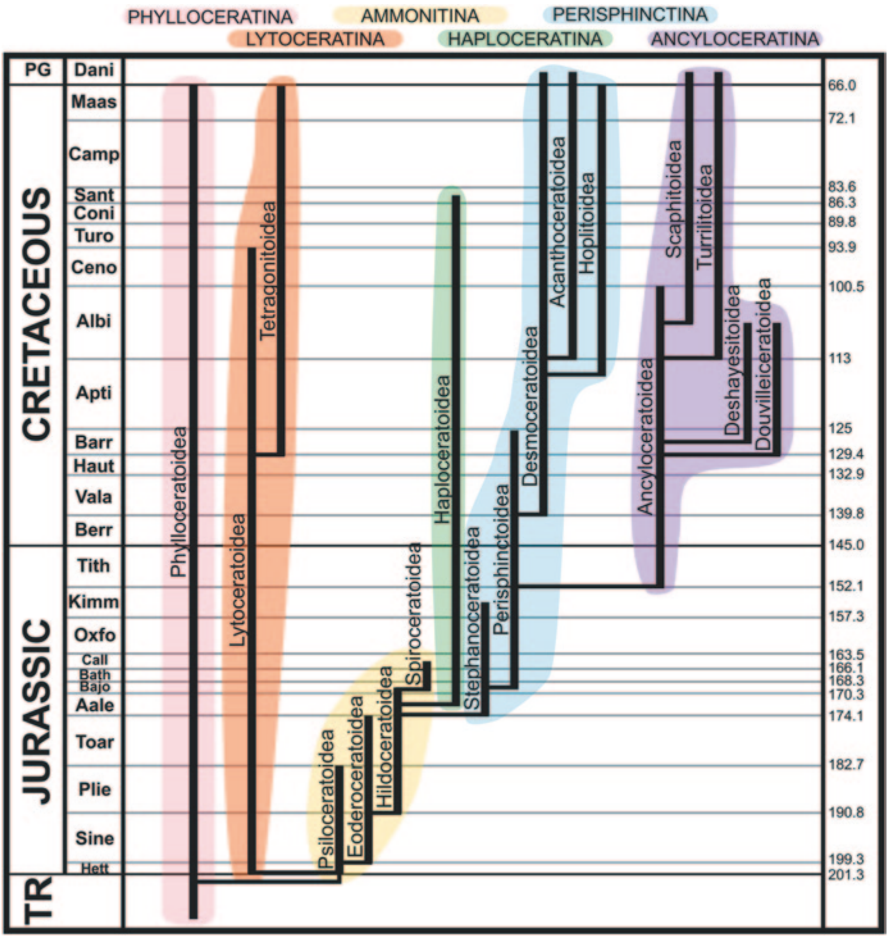
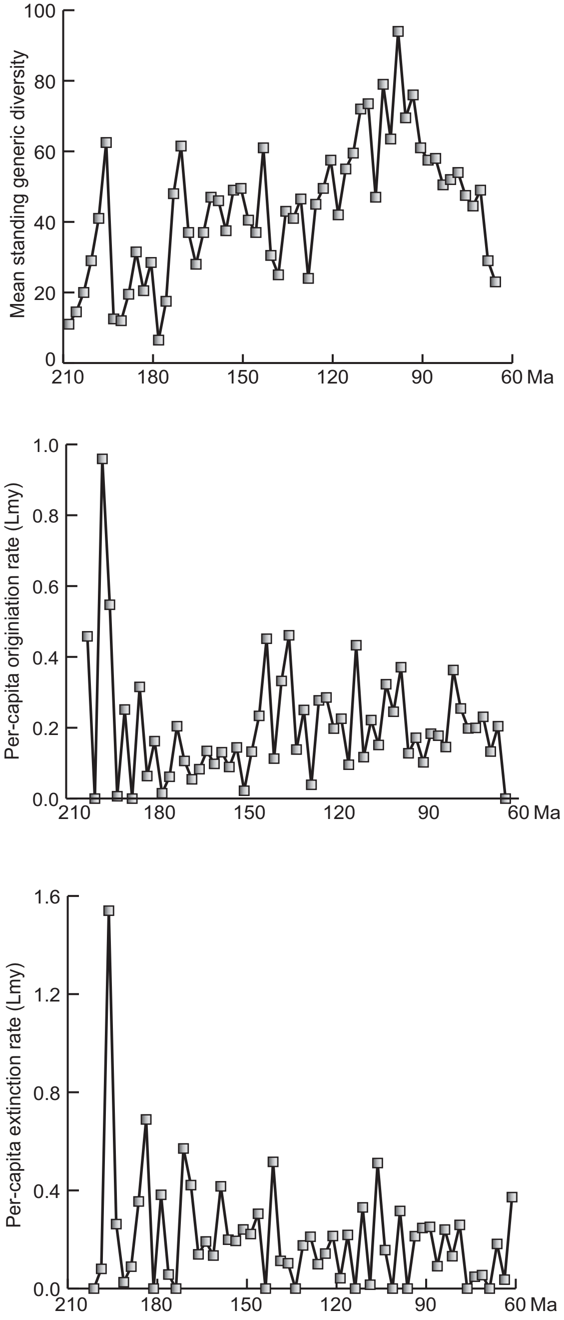


Fig. 8.1 Phylogenetic and stratigraphic context for Jurassic and Cretaceous ammonoid superfamilies. Suborders are indicated by shading, with corresponding suborder names arranged at *top* of figure. Stratigraphic ranges and phylogenetic relationships are synthesized from: Arkell et al. 1957; Schindewolf 1962; Houša 1965; Wiedmann 1969; Doguzhaeva and Mikhailova 1981; Donovan et al. 1981; Wright 1981; House 1988; Guex 1995; Page 1996; Wright et al. 1996; Engeser and Keupp 2002; Blau et al. 2008; Page 2008; Galácz 2012; Landman et al. 2012; Howarth 2013. Absolute time scale (right, in Ma) and stratigraphic stages (left) are derived from the 2013 Chronostratigraphic Chart of the International Commission on Stratigraphy (Cohen et al. 2013)

and extinction rates for J-K ammonoids averaging about 0.2 originations and extinctions per lineage-million years, though rates could be as high as 0.96 and 1.54 events per lineage-million years, respectively, for individual Early Jurassic substages (Fig. 8.2). By comparison, origination and extinction rates for marine metazoans as a group are typically less than 0.1 events per lineage-million years (Foote 2000).

Many have noted the relative evolutionary and morphological stability of the suborders Phylloceratina and Lytoceratina, relative to other ammonite suborders

Fig. 8.2 Diversity dynamics of Jurassic-Cretaceous ammonoids. **a** Mean standing generic diversity. **b** Per-capita origination rate in lineage-million years. **c** Per-capita extinction rate in lineage-million years. Generic diversity has been compiled at the substage level. Redrawn from Yacobucci (2005)



(Page 1996; but see Tanabe et al. 2003). The superfamily Desmoceratoidea (Perisphinctina) also shows a slower rate of evolution than other groups. Kennedy and Cobban (1976), for example, describe species longevities of 0.2–0.9 million years for Late Cretaceous ancyloceratines, while phylloceratine, lytoceratine, and desmoceratoid species show stratigraphic ranges from 8 to 25 million years. Possible explanations for this difference in evolutionary volatility among J-K ammonoid clades are discussed in Sect. 8.3.4.

The biodiversity history of J-K ammonoids is characterized by a distinctive "boom-and-bust" pattern of evolution and extinction, quite different from other mollusk classes (Vinarski et al. 2011). During the "boom" phase, a great variety of ammonoid taxa and morphotypes were produced in a very short interval. Higher taxa (families, superfamilies, and suborders) were established during these events. For instance, the initial Hettangian radiation of Early Jurassic ammonoids established Psiloceratoidea, Eoderoceratoidea, and Lytoceratoidea (Guex 1987), while Haploceratoidea, Stephanoceratoidea, and Perisphinctoidea appeared in the Middle Jurassic (Aalenian-Bajocian) diversification event (Donovan et al. 1981). Rapid radiations also occurred within superfamilies, notably in the Early Cretaceous for Desmoceratoidea (Hauterivian-Barremian) and Ancyloceratoidea (Aptian) and in the Late Cretaceous for Acanthoceratoidea and Hoplitoidea (Albian-Cenomanian) (Wright 1981). Biodiversity crashes were similarly frequent; these "bust" phases eliminated substantial proportions of the standing diversity of ammonoids. While virtually every stage and substage boundary of the Jurassic-Cretaceous interval is marked by at least regional ammonoid extinction events, more substantial extinctions also occurred, especially in association with ocean anoxic events (House 1985; Page 1996; Macchioni and Cecca 2002; Cecca and Macchioni 2004; Moyne et al. 2004; O'Dogherty et al. 2006; Moyne and Neige 2007; Dera et al. 2010, 2011; Hardy et al. 2012; but see Monnet et al. 2003, Monnet and Bucher 2007, and Monnet 2009 for a challenge to anoxia as the cause of the Cenomanian-Turonian turnover event). Hence, more or less distinctive ammonoid faunas characterize the Early Jurassic, Middle-Late Jurassic, Early-Mid Cretaceous, and Late Cretaceous. A few ammonoid species may have survived, if briefly, the end-Cretaceous extinction event (Machalski and Heinberg 2005; Landman et al. 2012).

8.2.3 Phylogenetic Analyses

The rapid evolution and extinction of ammonoids have made them valuable biostratigraphic index fossils. Their biostratigraphic utility, however, has hindered a more contemporary approach to their systematics. New ammonoid species are frequently described based on a stratophenetic view, in which species are initially distinguished by their stratigraphic occurrence, with anatomical features then identified as diagnostic for those groupings (Donovan 1994). Whether or not these groups are 'real' species in the biological sense may not be a concern for many biostratigraphers. However, to understand the macroevolution of ammonoids, a more rigorous, contemporary phylogenetic approach to document relationships among species must be employed (Rouget et al. 2004; Neige et al. 2007; Pardo et al. 2008; Yacobucci 2012; Bert and Bersac 2013).

Many cephalopod paleontologists have been reluctant to pursue a parsimony-based phylogenetic approach, in part because of the pervasive homeomorphy that characterizes many ammonoid groups (see Sect. 3.1 below). While homeomorphy is a concern in other mollusk classes as well (e.g., Schneider (2001) on bivalves; Schander and Sundberg (2001) and Wagner (2001) on gastropods), it is perceived as especially common in J-K ammonoids, which can make it difficult to separate convergent evolution from shared ancestry. Strategies do exist, however, to address homeomorphy, and rather than assuming it *a priori*, homeomorphy should be demonstrated by phylogenetic analysis. It may be that ammonoids are no more prone to homeomorphy than other groups, such as arthropods, bryozoans, and mammals, which are routinely subjected to phylogenetic analysis (Yacobucci 2012). It has also been shown that even homeomorphic characters still contain some phylogenetic signal (Poe and Wiens 2000).

The high levels of intraspecific variability shown by many J-K ammonoids represent another obstacle to phylogenetic analysis (see De Baets et al. 2015). A single ammonoid species may display morphological differences between specimens that might otherwise be used to diagnose separate genera (see Sect. 3.3 below). Such variability has been difficult to capture using standard phylogenetic techniques, although variable characters can now be coded as polymorphisms in most phylogenetic software programs. Perhaps a bigger challenge is determining which variable characters are phylogenetically meaningful and which represent non-phylogenetic processes such as ecophenotypic variation or taphonomic overprinting.

The majority of phylogenetic analyses of ammonoid clades have been conducted on Jurassic or Cretaceous groups, typically exploring relationships within a genus or family (Yacobucci 2012). A more comprehensive analysis to establish relationships among higher taxa has not been accomplished to date. Such an analysis, focusing not just on shell morphology but also on the timing of morphological development and life history traits, will be essential in order to rigorously test hypotheses about the tempo and mode of J-K ammonoid evolution.

8.3 Macroevolutionary Processes

8.3.1 Homeomorphy and Iterative Evolution

Homeomorphy here refers to the occurrence of similar shell forms in more or less distantly related groups. In ammonoids, the similarity is typically in shell shape and ornamentation, although suture patterns can also be similar in groups that are only distantly related (Schindewolf 1940; Haas 1942; Arkell et al. 1957; Kennedy and Cobban 1976; Saunders and Swan 1984; Dommergues et al. 1989; Dommergues

1994; Donovan 1994; Guex 2001; Monnet et al. 2011). Examples of homeomorphy have been particularly well-documented in ammonoids from the Jurassic (e.g., Dommergues et al. 1984; Dommergues and Mouterde 1987; Cariou et al. 1990; Meister 1993; El Hariri et al. 1996; Dommergues 2002; Cecca and Rouget 2006; Schlögl et al. 2006; Schweigert et al. 2012) and the Cretaceous (e.g., Reyment 1955; Obata 1975; Jeletzky and Stelck 1981; Delanoy and Poupon 1992; Maeda 1993; Kennedy and Wright 1994; Delanoy and Busnardo 2007; Bujtor 2010) Periods. Indeed, it is understood among J-K ammonoid workers that homeomorphy is to be expected when describing new species, and many taxonomic descriptions of ammonoid taxa therefore include sections on how to distinguish the new group from homeomorphs. Typically, the homeomorphic traits are restricted to adult forms, so homeomorphs can be distinguished by considering their entire ontogeny (Donovan et al. 1981). It should also be noted that modern coleoid cephalopods show extensive convergent evolution as well (Lindgren et al. 2012).

Iterative evolution involves similar-looking species repeatedly evolving through time. An early view among ammonoid workers was that many new J-K ammonoid groups were independently derived from Phylloceratina or Lytoceratina via iterative evolution, as deep water "root stocks" repeatedly gave rise to descendant forms inhabiting shallow shelves and epeiric seas. While this notion is no longer held by ammonoid paleontologists, at least for the origins of suborders and superfamilies (Wiedmann 1966; Donovan et al. 1981; Wright 1981), specific examples of homeomorphic evolution are frequently tied to sea level cycles. In particular, selection favoring certain morphs in certain habitats may be the most likely process driving the recurrent evolution of ammonoid homeomorphs. Seilacher and Gunji (1993) argued that certain shell shapes would be adapted to particular water depths, and therefore that parallel evolution of similar shell forms could be expected within shallow epeiric seas. Similar arguments relating homeomorphic shell forms to water depth and sea level cycles have been made by Bayer and McGhee (1984), Jacobs et al. (1994), Cecca and Pochettino (2000), Courville (2007), and Bujtor (2010). Courville (2007), for instance, proposed that Cenomanian-Turonian ammonites can be divided into (1) a cosmopolitan fauna adapted to life in open platform and shelf habitats and (2) groups of endemic ammonites that diversified within epeiric seaways (such as the Trans-Saharan Seaway of West Africa) during sea level highs. Each time sea level rose, a new group of seaway endemics evolved from open shelf ancestors. These endemics display homeomorphic adaptations to seaway habitats, with the same shell forms and ornaments recurring in each sea level cycle.

As an alternative to adaptation to particular water depths, Monnet et al. (2012) noted that repeated trends to larger shell size and increased shell coiling in Middle Triassic ammonoids might best be explained as a manifestation of Cope's Rule, the often-cited trend of increasing adult body size within a clade. De Baets et al. (2012) suggested that the opposite trend, towards smaller embryonic/hatchling size in at least three separate lineages of Devonian ammonoids, might represent adaptations for increased fecundity and higher mobility of hatchlings within the water column. These changes would have been favored during the Devonian 'Nektonic Revolution,' when free-swimming predators diversified. Such selection for larger or smaller adult sizes may also be applicable to J-K ammonoids, and is therefore in need of further exploration.

Finally, Guex (2000, 2001) has argued that environmental stress may be the root cause of homeomorphy in ammonoids. "[M]*ajor evolutionary jumps in ammonoids occur during severe extinction events, and are characterized by the sudden appearance of simple, primitive-looking forms which are atavistic with respect to their more complex immediate ancestors*" (Guex 2000, p. 115). For Guex, environmental stress preferentially causes more complex ammonoid forms to die out, while simpler forms that resemble distant ancestors evolve to take their place. In this view, homeomorphs are more likely to occur during or immediately after times of environmental perturbation and heightened turnover, and show atavistic or ancestral traits.

8.3.2 Heterochrony

The study of heterochrony in ammonoids extends back decades and is still an active area of inquiry (Dommergues et al. 1986; Landman 1988b; Marchand and Dommergues 1988; Korn 1992; Landman and Geyssant 1993; Gerber et al. 2007; Gerber 2011; Korn 2012). Both paedomorphosis (the retention of ancestral juvenile traits in the adult descendant) and peramorphosis ('overmaturation' of descendants past the ancestral adult form) have been described in ammonoids. Within the paedomorphic realm, progenesis (early sexual maturation) is most common, though examples of neoteny (slowed growth) have also been cited. Progenetic dwarfs have been described from the Jurassic (Cariou and Sequeiros 1987; Marchand and Dommergues 1988; Landman et al. 1991; Meister 1993; Mignot et al. 1993; Dommergues 1994; Linares and Sandoval 1996; Neige et al. 1997; Parent 1997, 1998), and Cretaceous (Kennedy 1977; Wright and Kennedy 1980; Kennedy 1988; Landman 1989; Kennedy and Cobban 1990a, b; Landman et al. 1991; Wright et al. 1996; Kennedy et al. 2001; Courville and Cronier 2003; Harada and Tanabe 2005) Periods. Peramorphosis is less common than paedomorphosis (Landman and Geyssant, 1993), and is often seen within taxa that also show paedomorphic changes, producing a mosaic form of heterochrony (Dommergues 1987; Linares and Sandoval 1996; Neige et al. 1997; Parent 1998; Courville and Cronier 2003).

Paleontologists have connected heterochronic patterns with other aspects of ammonoid paleobiology. For example, differences between sexual dimorphs (i.e., macroconchs and microconchs) have been related to heterochronic shifts. Tintant (1963), Guex (1981), and Parent (1997) all suggested microconchs were produced by progenesis or neoteny. Neige (1992) also identified progenesis as the source of some microconchs among Jurassic ammonites, but additionally recognized hypomorphosis as a contributing process in some taxa.

Paleobiologists have argued that certain heterochronic changes would be adaptively favored in particular environments. For instance, progenesis could be advantageous in unstable environments, as rapid maturation would allow individuals to exploit abundant juvenile resources. Neoteny (slowed growth), in contrast, would be favored in more stable environments (Gould 1977; Wiedmann 1988; McKinney and McNamara 1991). Many examples exist that document this relationship between heterochronic evolution and environmental stability. Mancini (1978) argued that the progenetic dwarfs of the Cretaceous Grayson Formation of Texas were better adapted than their larger ancestors to live on the unusually soft substrates present at that time. Alternatively, Enay and Gygi (2001) suggested that the Jurassic progenetic dwarfs they investigated would have been more tolerant of dysoxic bottom waters. In a similar vein, Mignot et al. (1993) argued that paedomorphosis within the Early Jurassic ammonoid *Hildoceras* was an adaptive response to sub-optimal environmental conditions, and Zatoń (2008) suggested that the range of mature body sizes seen in Jurassic tulitids was due to varying environmental conditions. Monnet et al. (2003) argued that paedomorphic changes resulting in smaller adult body sizes during the Late Cenomanian were driven by environmental perturbations such as sea level rise, temperature increase, and productivity changes. Stevens (1988) suggested that large adult body sizes (as are produced in certain heterochronic shifts such as neotenic or hypermorphic gigantism) might be expected in cold, deep-water environments. Landman and Geyssant (1993) reviewed 167 reported cases of heterochrony in ammonoids, relating the different heteromorphic processes to different modes of life (e.g., nektobenthic, oceanic, megaplanktonic). While paedomorphosis still predominated, neritic nektobenthic forms were more likely to show peramorphosis than other ecologies. Vertical migrators showed the highest rate of progenesis.

The prevalence of heterochrony among ammonoid clades has also been related to diversification rates and the production of species and higher taxa. As a Paleozoic example, Korn (1995) argued that the diversification of several Late Devonian goniatite and clymeniid clades was driven by sea level fluctuations that favored accelerated maturation and reproductive rates during times of relative sea level fall. Marchand and Dommergues (1988) suggested that the evolution of new ammonoid lineages in the Jurassic was associated with progenesis, while subsequent evolution within lineages was due to neoteny or acceleration. Geyssant (1988) also argued that progenesis produced new species, citing changes in homeotic genes controlling growth as the source for morphological novelty. Yacobucci (1999) linked the rapid endemic radiation of acanthoceratid ammonoids in the Late Cretaceous Western Interior Seaway of North America to their developmental flexibility, highlighting the prevalence of progenetic offshoots within this group. Landman (1989) noted that repeated instances of progenesis produced different ammonoid species that had nearly identical juvenile forms, but diverged at maturity. Landman et al. (1991) emphasized that the various Jurassic and Cretaceous progenetic species were not merely sexually mature juveniles, but also had unique mature traits that make them diagnosable taxa. They argued that this "novel combination of juvenile, adult, and unique features may endow progenetic species with the evolutionary potential to play a role in the origin of higher taxa." (Landman et al. 1991, p. 409).

Homeomorphic evolution has also been linked to heterochrony by several workers. Dommergues et al. (1989) argued that homeomorphy of shell forms in various Jurassic ammonoids was due to heterochronic processes that recurrently produced similar shell morphologies (e.g., disk-shaped oxycones, globular sphaerocones). Both Landman (1989) and Dommergues (1994) specifically cited iterative progenesis as the mechanism producing smaller-bodied species that resembled the juveniles of older or co-occurring ammonoid species. These progenetic trends repeated several times, producing similar-looking species –homeomorphs– in each iteration. Similarly, Meister (1993) suggested that paedomorphosis by neoteny was responsible for producing homeomorphic suboxyconic shell forms in multiple groups of Early Jurassic phylloceratine ammonoids.

8.3.3 Developmental Flexibility

In addition to heterochronic processes, various other forms of developmental flexibility have been documented in ammonoids and used for systematic purposes. This developmental flexibility may help explain the extreme intraspecific morphological variability that is seen in many J-K ammonoid groups (e.g., Reeside and Cobban 1960; Westermann 1966; Kennedy and Cobban 1976; Howarth 1978; Meléndez and Fontana 1993; Yacobucci 1999, 2003; 2004a, b; Morard and Guex 2003; Kakabadze 2004; Gangopadhyay and Bardhan 2007; Gerber et al. 2008; Reyment 2011; Knauss and Yacobucci 2014; De Baets et al. 2015). Certainly the sexual dimorphism that characterizes many J-K ammonoid species (Kennedy and Cobban 1976; Callomon 1981; Donovan et al. 1981; Davis et al. 1996) must relate to variations in the developmental growth program.

Perhaps not surprisingly, then, ammonoid paleontologists have been pioneers in the use of developmentally defined characters in systematics. The systematic description and differentiation of ammonoid species often includes reference to developmentally-based characters. One species of a genus might reach maturity at a smaller size than another. Features of ornamentation like ribs and tubercles may occur only on one portion of the shell, indicating a developmental shift in the shell's growth program. Traits like the density of ribs or the shape or pattern of spacing of tubercles may change during growth. The adult suture may remain relatively simple in one species while developing more complexity through ontogeny in a close relative. Characters like these are routinely used to diagnose and differentiate closely related ammonoid species. By contrast, systematists who study extant animals more rarely use juvenile traits and aspects of developmental timing in their work. Recently, modern biologists have argued that variations in developmental timing may be a driver of speciation, as they provide a source for new innovations, populational polyphenism, and pre-mating isolation mechanisms (Naisbit et al. 2003; West-Eberhard 2003, 2005; Minelli and Fusco 2012). Ammonoid paleontologists are well-situated to lead integrative research efforts on the role of developmental flexibility in speciation and the production of higher taxa.

8.3.4 Environment and Evolution

Ammonoid paleontologists have long argued that environmental factors, like sea level changes, water temperature, and oxygen content, had a primary impact on evolutionary dynamics, including incidents of homeomorphy and heterochrony, as noted above (Ziegler 1967; Kennedy and Cobban 1976; Futukami and Obata 1988; Marcinowski and Wiedmann 1988; Meléndez et al. 1988; Wiedmann 1988; Hallam 1989; House 1989, 1993; Hantzpergue 1991, 1995; Ross et al. 1992; Rawson 1993; Wiedmann and Kullmann 1996; Bengtson and Kakabadze 1999; Yacobucci 1999; Hirano et al. 2000; Sandoval et al. 2001, Navarro et al. 2005; Olóriz and Villaseñor 2006; Bardhan et al. 2007; Bourillot et al. 2008; Lehmann and Herbig 2009; Ifrim and Stinnesbeck 2010; Nagm and Wilmsen 2012; Ruban 2013). Biotic factors such as changes in plankton food sources were likely also important (Kruta et al. 2011; Ohkouchi et al. 2013). Ammonoids were subject to a variety of selective pressures, which likely varied both spatially and temporally. Key environmental variables may have occurred as spatial gradients (e.g., water depth, temperature, salinity, dissolved oxygen) or as more discrete patches (e.g., nutrients, substrate types), especially within epeiric seas. Ammonoid populations and species would necessarily respond to changes in these environmental parameters, whether by extinction, migration, or adaptive evolution.

The ammonoid suborders Phylloceratina and Lytoceratina and the superfamily Desmoceratoidea are characterized by relative evolutionary stability and morphological conservatism (Arkell et al. 1957; Page 1996; Neige et al. 2013; but see Bourillot et al. 2008). It has been argued that this stability stems from their more environmentally stable, open ocean habitats (House 1989; Tanabe et al. 2013). Ammonoids living in shallow shelves and epeiric seas, on the other hand, show higher taxonomic and morphological diversity and higher evolutionary turnover, presumably as a response to more unstable environmental conditions (Ziegler 1981).

This documented difference in evolutionary rates between deep open ocean and shallow restricted shelf/sea habitats has led paleontologists to tie ammonoid evolution to sea level cycles (Wiedmann 1973; Kennedy and Cobban 1976; Hirano 1988; Yacobucci 1999). Slowly evolving groups living offshore would provide the initial species that invaded newly created or accessible onshore habitats during transgressions. An adaptive radiation would ensue, producing many new ammonoid species during a short time interval. When sea level later fell, these shallow water species would rapidly become extinct. Then, when sea level rose again, a new suite of ammonoid species, derived from the stable offshore species, would radiate into shallow habitats once more.

Case studies of specific examples of this evolutionary pattern have revealed more complexity in the evolutionary processes involved. Hirano (1988), for instance, explored the evolution of the Cenomanian desmoceratids *Desmoceras* and *Tragodesmoceroides* and the tetragonitid *Gaudryceras* from Japan. He found species-level stasis over several million years in the open ocean *Desmoceras* (*P.*) *japonicum*, which then gave rise to *Tragodesmoceroides subcostatus* via relatively rapid allopatric speciation. *Gaudryceras*, on the other hand, showed episodes of increased polymorphism within a species, rather than the divergence of a new species. Macchioni and Cecca (2002) argued that both transgressions and regressions could change regional biodiversity and the degree of endemism in Early Jurassic ammonoid faunas. Lukeneder (2012) found that both abundance and diversity peaked during highstands in Early Cretaceous (Hauterivian-Barremian) ammonoids from the Italian Alps; the possibility that higher abundances influenced biodiversity counts is an open question.

Further complicating the link between sea level cycles and ammonoid diversity dynamics is the association of sea level highstands with episodes of ocean anoxia. Rising sea levels may be associated with global warming and a reduction in thermohaline ocean circulation. The rising seas may also bring the oxygen minimum zone up in the water column such that it impinges on the shallow seafloor. Such times of anoxia or dysoxia are known to be associated with ammonoid extinctions and turnover. Hirano et al. (2000), for example, documented the stratigraphic ranges of 902 Cretaceous ammonoid species from Japan. They found a diversity peak in the Late Albian, with lower diversities during mid-Cretaceous ocean anoxic events. Turnover among ammonoids during the Pliensbachian-Toarcian (Early Jurassic) has long been associated with ocean anoxia (Macchioni and Cecca 2002; Rulleau et al. 2003; Dommergues et al. 2009; Dera et al. 2011). Hence, ammonoid extinction may be elevated both at times of sea level rise and sea level fall, depending on the circumstances (Becker 1993; Korn 1995; Yacobucci 1999).

It may also be that sea level cycles and their associated environmental changes drive origination as well as extinction. Transgressions produce new habitat space, which may trigger adaptive radiations within a few invading higher taxa. Regressions may isolate previously connected regions and promote allopatric speciation (Yacobucci 1999, 2015).

8.3.5 Speciation Models

Few invertebrate paleontologists have explicitly connected the species they study with any particular species concept (such as the biological or phylogenetic species concepts; Allmon and Smith 2011). Dozens of different definitions of species exist in the scientific literature. The Biological Species Concept (BSC) is certainly the most widely cited (e.g., it is the species definition found in most introductory textbooks). The BSC states that species are groups of interbreeding natural populations that are reproductively isolated from other groups (Mayr 1942, 1963; 1995. While it is impossible to apply this definition directly to fossil species, it does express the core theoretical concept that species are distinct, isolated gene pools, each therefore with its own unique evolutionary history.

The ‘reality’ of species as distinct evolutionary units can be difficult to demonstrate, for living and extinct organisms alike. The paleontological morphospecies concept infers that morphological similarity should reflect evolutionary proximity

(Raup and Stanley 1978, p. 130). Given the prevalence of homeomorphy in J-K ammonoids, this inference may not always hold. The stratophenetic approach many workers have taken to J-K ammonoid classification means that nominal ammonoid species may or may not reflect "real" biological species. A tendency to oversplit highly variable ammonoid species further complicates our understanding of ammonoid diversity. In addition, Nardin et al. (2005) found that Jurassic ammonoid workers more readily named extreme forms than intermediate ones. Several workers (Kennedy and Wright 1985; Hallam 1990) have, indeed, suggested that ammonoid genera may be closer to "real" species than the nominal species are. Ideally, future workers will at least more explicitly describe the species concept they are using.

The speciation process has been intensively studied by modern biologists for decades. Proposed speciation mechanisms differ primarily in their geographic context and the degree of gene flow permitted between diverging populations. Allopatric speciation is widely accepted as the most common mode of speciation (Mayr 1942, 1963, 1995; Lieberman 2000; Coyne and Orr 2004; Marie Curie SPECIATION Network 2012; Nosil 2012). In the allopatric speciation model, lack of gene flow between populations is due to geographic separation. How much geographic separation is necessary to prevent gene flow is a function of the organisms' mobility and dispersal ability; allopatric speciation is known to occur across small geographic scales in shallow marine settings (Meyer et al. 2005; Krug 2011). Parapatric speciation involves populations occupying an ecological gradient that experience ecological divergence as each population adapts to its local environments; some gene flow can still occur between adjacent populations (Coyne and Orr 2004; Nosil 2008; Pinho and Hey 2010; Keller and Seehausen 2012). Sympatric speciation, in which populations show extensive geographic overlap and gene flow, has remained controversial, in part because the definition has shifted over time from a purely geographic one to one that focuses on the degree of gene flow between populations (Gavrilets 2003; Coyne and Orr 2004; Mallet 2008; Fitzpatrick et al. 2008, 2009; Mallet et al. 2009; Bird et al. 2012). One argument against sympatric speciation is that incipient species would occupy the same ecological niche and therefore one population would just out-compete the other, driving it to extinction before it can successfully diverge into a new species. Successful sympatric speciation, then, requires simultaneous reproductive isolation and ecological differentiation (Johannesson 2001; Coyne and Orr 2004), which could be produced by modifying certain traits that affect both the organisms' ecology and reproduction [coined "*magic traits*" by Gavrilets (2004)].

It has been suggested that these different speciation models may not be mutually exclusive; rather, speciation may involve an early allopatric stage when divergence begins and a later sympatric stage as the diverging population moves back into its parent population's range (Rundle and Schluter 2004; Rundle and Nosil 2005; Butlin et al. 2008; Aguilée et al. 2011; Marie Curie SPECIATION Network 2012). Parapatric speciation and mosaic sympatry (involving randomly distributed habitat patches within the overlapping ranges of diverging populations) may also be common (Mallet 2008; Mallet et al. 2009). Certainly, the speciation process typically takes place over tens of thousands of years, so populations are likely to experience a variety of geographic and environmental changes before becoming completely separate species (Norris and Hull 2012).

Rapid evolutionary radiations that involve frequent speciation, often within newly exploited habitats, provide a particularly interesting perspective on how speciation happens (Gavrilets and Losos 2009). The adaptive radiation of *Anolis* lizards in the Caribbean resulted in frequent parallel evolution of homeomorphic forms on different islands, suggesting that similar anatomical traits can evolve repeatedly within a clade that encounters similar environments (Mahler et al. 2013). Studies of Galápagos finches (Grant et al. 2006; Grant and Grant 2008) and cichlid fish (Albertson and Kocher 2006) have shown the importance of developmentally plastic traits as the source for anatomical variation involved in ecological divergence of rapidly speciating populations. The African cichlid fish radiations demonstrate the importance of both environmental factors and sexual selection on lineage-specific traits for fueling speciation (Wagner et al. 2012).

Ammonoid workers have primarily addressed the speciation process indirectly, by assessing the dispersal ability of ammonoids as juveniles. Mesozoic ammonoids had small eggs (0.5–2.6 mm) and hatchling sizes, and probably spent some time in the plankton during the early juvenile phase of their life cycle, before settling into a nektic or nektobenthic habit (Landman 1988a, Landman et al. 1996; Shigeta 1993; Tajika and Wani 2011). It should be noted, however, that ammonoid taxa associated with deep and cold water habitats (e.g., Phylloceratina, Lytoceratina) had larger eggs than taxa in shallow and warm water habitats (e.g., Ammonitina, Ancyloceratina; Laptikhovsky et al. 2013), so a planktonic juvenile phase may not have been universal among J-K ammonoids. Many examples exist of juvenile and adult ammonoids living in separate habitats (Kennedy and Cobban 1976; Morton 1988; Tsujita and Westermann 1998). Tajika and Wani (2011) studied hatchling size in species of *Gaudryceras* (Lytoceratina) and *Hypophylloceras* (Phylloceratina) from the Late Cretaceous of northern Japan, and estimated they were planktonic for at least five days. Ikeda and Wani (2012) and Yahada and Wani (2013) found that adult shell thickness ratios (width/diameter) change with depth within a wide range of ammonoid species while juvenile proportions do not; they interpreted this finding as evidence for planktic hatchlings and nektobenthic adults. Wani (2011) documented hatchling sizes in ammonoids and nautiloids throughout the Phanerozoic and compared them to those of modern cephalopods. He found that ammonoids showed consistently small hatchling sizes (<3 mm) through time, while nautiloid hatchling sizes increased in the Jurassic to their presently-observed size of 22–33 mm. Modern cephalopod hatchling size is related to planktonic (<3 mm) vs. nonplanktonic (>10 mm) habits. Hence, while J-K nautiloid hatchlings were likely nonplanktonic with limited dispersal and more restricted geographic ranges, J-K ammonoid hatchlings were likely planktonic with greater dispersal ability and larger geographic ranges. Wani (2011) concluded that sympatric speciation was more likely than allopatric speciation in ammonoids. However, while these studies support the possibility of sympatric speciation, we need more complete and detailed data on the geographic ranges of J-K ammonoid species, as well as careful mapping of possible microhabitats or mosaic habitats in shallow shelf and epeiric sea settings, to determine whether sympatric or allopatric speciation actually took place within a given ammonoid clade.

8.4 Role of Paleobiogeography in Macroevolution

8.4.1 The Mesozoic Earth System

The Mesozoic Earth System was marked by significant tectonic, oceanographic, and climatic changes. The supercontinent Pangea began rifting apart by the Early Jurassic, first with the opening of the North and Central Atlantic (Labails et al. 2010; Ruiz-Martínez et al. 2012) and later by the opening of the Hispanic Corridor, which produced an ocean passage connecting Western Tethys with the Eastern Pacific (Fig. 8.3a). No direct geological evidence exists for the Hispanic Corridor prior to the late Middle Jurassic, although a flooded rift zone that permitted ammonoid dispersal between Tethys and the Eastern Pacific could have been present earlier (Longridge et al. 2008). The Gondwanan continents separated later, in the Early to Mid-Cretaceous, with the South Atlantic opening from south to north beginning in the Hauterivian (Fig. 8.3b) (Owen and Mutterlose 2006; Rawson 2007; Torsvik et al. 2009; Geraldes et al. 2013).

High sea levels through the J-K interval (Haq et al. 1987, 1988) flooded large areas of the continents and offered marine connections between these opening ocean basins. The dispersal of Jurassic ammonoids through the Hispanic Corridor (Fig. 8.3a; Smith and Tipper 1986; Moyne et al. 2004; Arias 2008; Longridge et al. 2008; Fernández-López and Chong Díaz 2011; Galácz 2012; Stevens 2012; Sandoval et al. 2013) and Cretaceous ammonoids through the Trans-Saharan Seaway (Fig. 8.3b; Reyment 1980; Meister et al. 1992, 1994; Courville et al. 1998; Courville 2007; Lehmann and Herbig 2009; Nagm et al. 2010; Nagm and Wilmsen 2012) have been particularly well-documented. Rising sea level was driven both by increases in mid-ocean ridge volume and by global warming. Generally warm "greenhouse" conditions prevailed for most of the Jurassic and Cretaceous, although climate did vary through this interval. The Early and latest Cretaceous have been characterized as a "cool greenhouse" (with mountain glaciers and small volumes of at least seasonal polar ice) while ocean anoxic events (OAEs) during the Triassic-Jurassic transition, Toarcian, Aptian, and Cenomanian-Turonian intervals can be linked to extreme hothouse conditions, driven in part by the eruption of large igneous provinces (Kidder and Worsley 2010, 2012; Takashima et al. 2011; Hay and Floegel 2012). Hence, tectonics, climate, and sea level are strongly linked within the Earth System throughout the Jurassic and Cretaceous Periods.

The breakup of Pangea has long been thought to drive global biodiversity increases by increasing provinciality, with geographic isolation leading to higher origination rates for species and higher taxa (Valentine et al. 1978). However,

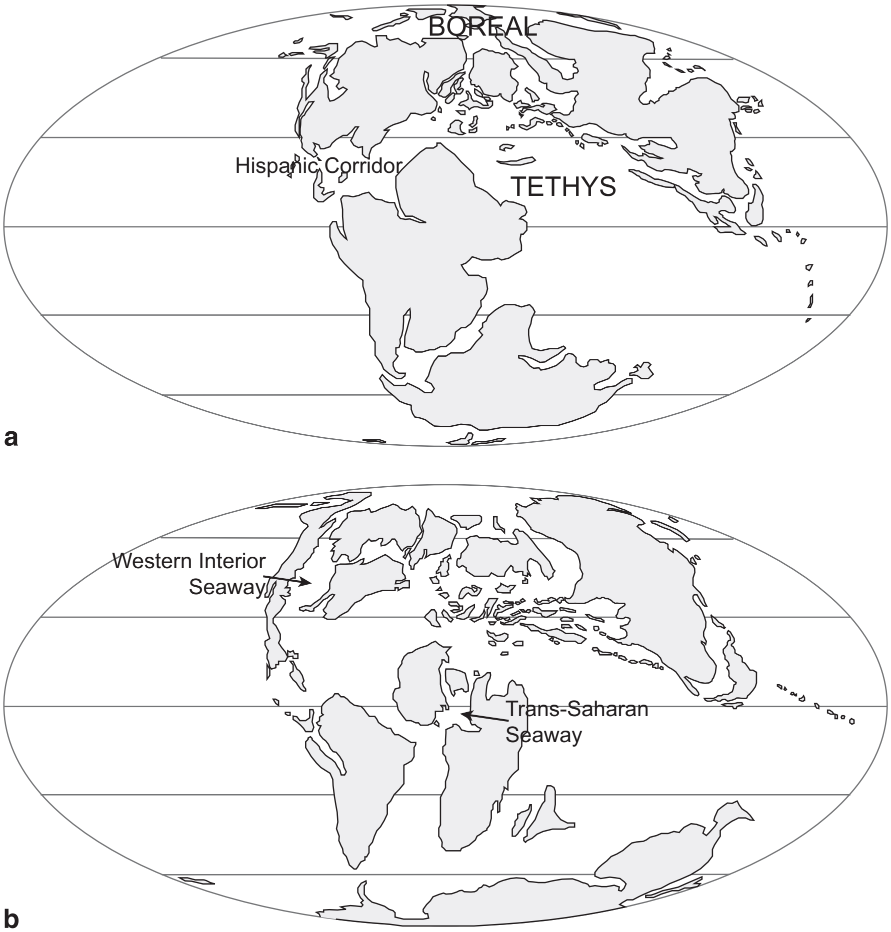


Fig. 8.3 Mesozoic paleogeography. **a** Late Jurassic (150 Ma). **b** Late Cretaceous (90 Ma). Mollweide projection. Maps redrawn from Blakey (2011a)

Miller et al. (2009) found, using a standardized dataset of brachiopod, bivalve, and gastropod occurrences derived from the Paleobiology Database, no increase in "*geo-disparity*" (i.e., faunal compositional differences as a function of geographic distance) through the Phanerozoic. On the other hand, they also found that the Mesozoic showed a unique pattern. Rather than the expected decreasing faunal similarity with geographic distance that was seen for the Paleozoic and Cenozoic Eras, the Mesozoic data showed an irregular relationship between these variables, implying greater cosmopolitanism among Mesozoic groups. Miller et al. (2009) suggested that Mesozoic settings were especially "*patchy,*" with epeiric seas, ocean-facing shallow shelves, and small land masses intermingled, most notably within Tethys. Given the longstanding belief that ammonoid diversity is linked to sea level and tectonics, a similar analysis focusing on the Mesozoic ammonoid occurrence record would make a useful comparison to that of Miller et al. (2009).

8.4.2 Ammonoid Paleobiogeography

Before discussing the paleobiogeography of ammonoids and its role in the macroevolution of this group, we must consider whether significant postmortem drift affected the geographic distribution of fossil remains, and therefore whether geographic patterns documented in the fossil record can be used to infer biological processes. Shells of modern *Nautilus* are known to drift substantial distances beyond their living range within the Indo-Pacific region (Reyment 1958, 1973; Toriyama et al. 1965; House 1987), a process supported by findings in experimental and observational taphonomy (Wani 2004, 2007; Mapes et al. 2010a, b). This propensity for postmortem dispersal has been inferred to apply to ammonoids as well (Reyment 1958, 2008; House 1987). Reyment (2008) reviewed the "*classical literature*" on the question of postmortem drift and concluded that "*nekroplanktonic dispersal is the rule rather than the exception*". However, Kennedy and Cobban (1976) and Cecca (1999), while acknowledging that post-mortem drift of dead ammonoid shells can happen, suggest it is possible to eliminate substantial drift in many specific cases. In particular, Kennedy and Cobban (1976) argued against postmortem drift by noting the large numbers of intact ammonoid specimens that are typically recovered from a fossil locality; they suggest postmortem drift is inadequate to explain these numbers. Maeda and Seilacher (1996) presented hydrostatic models that suggested a depth limit (which they left unspecified), below which dead ammonoid shells were likely to sink quickly and above which they were likely to float and drift in surface currents. This interpretation is supported by the occasional association of jaws with J-K ammonoid shells recovered from offshore settings (Tanabe et al. 2015). Hence, ammonoids living in shallow and/or surface waters might be more likely to experience post-mortem drift than deep water groups. Given the range of arguments on either side, the recommended best practice is to gather taphonomic evidence to support or refute postmortem drift for each particular case.

Ammonoid workers through the nineteenth and much of the twentieth centuries believed that J-K ammonoids were able to freely disperse across wide geographic distances, due to their nektonic mode of life. However, evidence has accumulated to support the view that many ammonoid species and genera were limited to relatively narrow geographic ranges, and show a significant degree of provincialism (Gordon 1976; Ziegler 1981; Thierry 1988; Marcinowski and Wiedmann 1988; Wiedmann 1988; Cecca 1999; Reboulet 2001; Macchioni and Cecca 2002; Cecca et al. 2005b; Dommergues et al. 2009; Dera et al. 2011; Yahada and Wani 2013). Kennedy and Cobban (1976) argued that many eurytopic ammonoid taxa had global distributions, due either to the dispersal by surface currents of planktonic hatchlings (see Sect. 3.5) or to active swimming of nektonic adults, while other ammonoids had limited temperature tolerances, restricting them to certain latitudes. They suggested that endemic ammonoid taxa are typically low-diversity, highly variable species that were prevented by geographic or environmental barriers from dispersing.

The geographic distributions of J-K ammonoids fluctuated through time. Sea level changes are widely thought to drive shifting geographic distributions, although local and regional barriers to dispersal are also important (Hancock and Kennedy 1981; Atrops and Meléndez 1988; Futakami and Obata 1988; Kotetichvili 1988; Meléndez et al. 1988; Hantzpergue 1991, 1995; Bengtson and Kakabadze 1999; Navarro et al. 2005; Olóriz and Villaseñor 2006; Moyne and Neige 2007; Sarih et al. 2007; Bourillot et al. 2008; Mitta 2008; Dommergues et al. 2009; Ifrim and Stinnesbeck 2010; Jagt-Yazykova 2011; Jagt-Yazykova and Zonova 2012). Early Jurassic ammonoids show a relatively cosmopolitan distribution, with the degree of provincialism increasing from the Middle Jurassic through the Middle Cretaceous (Gordon 1976; Westermann 2000). By the Middle Jurassic, two major biorealms—the Boreal and Tethyan Realms—are clearly established (Fig. 8.3a) (Kennedy and Cobban 1976; Rawson 1981; Westermann 2000). The Boreal Realm encompassed mid to high northern paleolatitudes while the Tethyan Realm spanned equatorial regions and the north and south margins of the Tethys Ocean. The Boreal Realm can be subdivided into Arctic and Boreal-Atlantic/Northwest Europe provinces while the much larger Tethyan Realm is varyingly divided into numerous provinces, including the Tethyan proper, West Tethyan, Mediterranean, Indo-Pacific, Indo-Madagascan, Andean, and Austral (southern high latitudes) provinces (Westermann 1981, 2000; Enay and Cariou 1997, 1999; Aguirre-Urreta et al. 2007; Bardhan et al. 2007; Obata and Matsukawa 2007). The East Pacific (i.e., localities in Western North and South America) is separated out as a third realm by some workers (Thierry 1976; Westermann 1981). Moyne et al. (2004) identified 16 ammonoid biogeographic provinces for the Middle Jurassic (Late Aalenian-Middle Bathonian; Fig. 8.4 top). They compiled global species diversity data for 23 ammonoid subfamilies, which produced a cluster diagram showing faunal similarities among regions (Fig. 8.4 bottom). Western Tethys and Circum-Pacific (including the Americas, Antarctic Peninsula, northeastern Pacific, Australia and New Zealand) groups were clearly defined. The Boreal Province was very distinct from all other regions, due to the dominance of the cardioceratid subfamily Arctocephalitinae, which was restricted to high latitudes.

Of particular interest to ammonoid paleontologists has been the European interface between the Boreal and Tethyan Realms. This interface shifted north and south throughout the Jurassic and Cretaceous, and varied from a relatively hard biogeographic boundary (with little mixing of faunas) to a much more porous boundary that permitted considerable mixing of Boreal and Tethyan ammonoid faunas, creating a distinctive European fauna (Callomon 1985, 2003; Thierry 1988, 2003; Cecca et al. 2005a; Alsen 2006; Wierzbowski and Rogov 2011). Provincialism within these larger realms also varied through time and could be strong (Cecca 1999).

A cooling interval in the Late Early Cretaceous (Late Aptian to Albian) redistributed ammonoids in the Pacific province (Iba and Sano 2007; Iba 2009; Matsukawa et al. 2012). As sea level peaked in the Mid-Cretaceous (Haq et al 1987, 1988), provincialism declined overall, although newly formed epeiric seaways such as the Western Interior Seaway of North America and the Trans-Saharan Seaway of Africa hosted radiations of endemic ammonoid clades (Kennedy and Cobban 1976; Marcinowski and Wiedmann 1988; Wiedmann 1988; Meister et al. 1992,

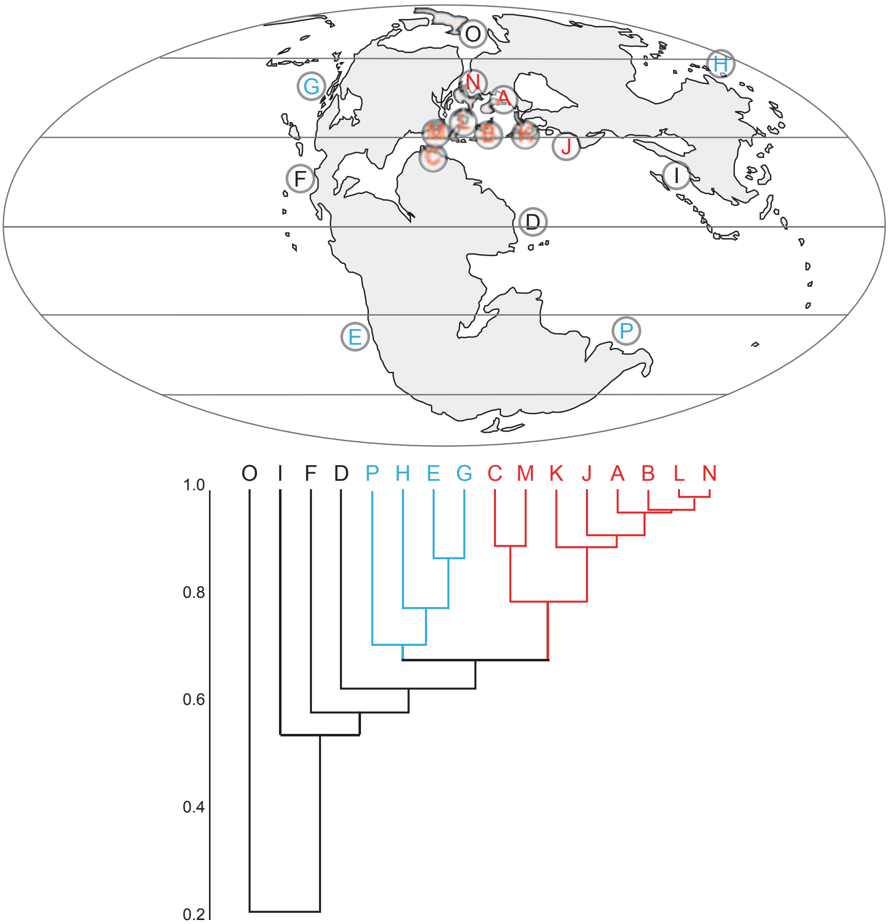


Fig. 8.4 Middle Jurassic ammonoid paleobiogeography. Sixteen biogeographic provinces were identified for the Middle Jurassic (late Aalenian-Middle Bathonian) by Moyne et al. (2004) (*top*), who produced a hierarchical ascendant classification from data on subfamily diversity in each province (*bottom*). They identified a Western Tethys group (in *red*) and a Circum-Pacific group (in *blue*). Note the pronounced difference between the Boreal province (*O*) and all other provinces, reflecting the dominance of the high-latitude cardioceratid subfamily Arctocephalitinae. Provinces: *A* North Mediterranean, *B* Middle Mediterranean, *C* Southwest Tethyan Margin, *D* South Tethyan Margin, *E* South America and Antarctic Peninsula, *F* Central America, *G* Western North America, *H* Japan and Eastern Russia, *I* Tibet and Southeast Asia, *J* Northeast Tethyan Margin, *K* North Tethyan Margin, *L* Southern Northwest European Platform, *M* Atlantic Basins, *N* Northern Northwest European Platform, *O* Boreal, *P* Austral. Province localities and cluster diagram redrawn from Moyne et al. (2004). Base map for Middle Jurassic (170 Ma) redrawn from Blakey (2011a)

1994; Courville et al. 1998; Yacobucci 1999, 2003; Monnet 2009; Nagm and Wilmsen 2012). By the latest Cretaceous, ammonoid faunas were becoming more geographically differentiated again, at least in shallow water settings (Gordon 1976; Rawson 1981; Kennedy et al. 1998; Olivero and Medina 2000). Zakharov et al. (2012), investigating Maastrichtian ammonoids and belemnites recovered from the

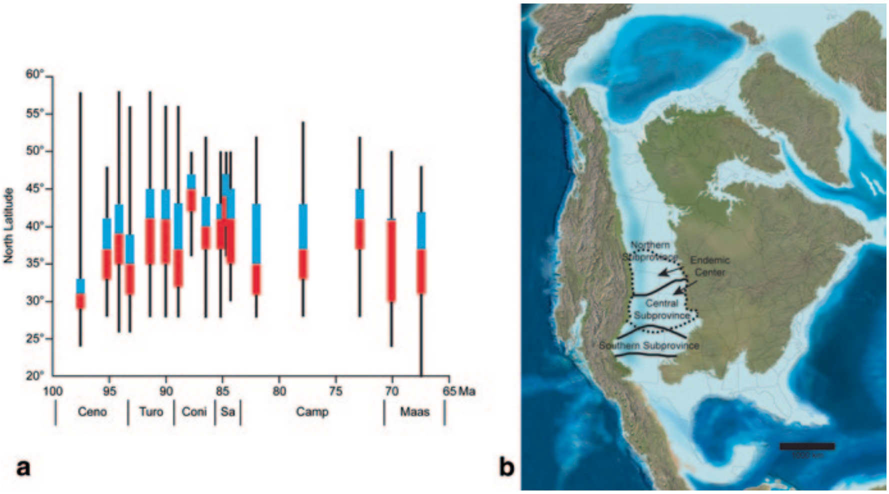


Fig. 8.5 Ammonoid paleobiogeography of the Late Cretaceous Western Interior Seaway of North America. **a** Diversity gradients per substage, based on counts of ammonoid genera present in 2° latitude bins. Box-and-whisker plots show minimum and maximum latitudes occupied (ends of *black lines*) and quartiles for generic diversity; median is marked by the boundary between the *blue* and *red boxes*. Note the northward shifts in diversity during the Cenomanian and Campanian global sea level rises. Stage abbreviations: Ceno-Cenomanian, Turo-Turonian, Coni-Coniacian, Sa-Santonian, Camp-Campanian, Maas-Maastrichtian. Absolute ages from Cobban et al. 2006. **b** Map of the North American Western Interior Seaway during the Late Cretaceous showing biogeographic provinces of Kauffman (1984). *Solid lines* are province boundaries; *dashed lines* show extent of endemic center. The endemic center, where the southern, central, and northern provinces overlapped, was home to a variety of endemic ammonoids. Map modified from 85 Ma North American reconstruction of Blakey (2011b)

mid-Pacific Magellan Seamounts, found evidence of mixing of ammonoids from middle and high northern latitudes into these deeper tropical waters. It may therefore be that open oceanic and/or deeper water ammonoids retained a cosmopolitan distribution through the Late Cretaceous.

Many studies of ammonoid paleobiogeography are essentially descriptive (what Dommergues and Marchand (1988) call an “*approche phénétique*”), documenting taxonomic occurrences in various regions and at various times. Such studies are critical for building comprehensive datasets of ammonoid occurrences through time, and have been used as input data for paleoceanographic models (e.g., Arias 2008). Interest is growing, however, in linking the spatial distributions of ammonoids to the underlying processes that control these distributions (Dommergues and Marchand’s (1988) “*approche causale*”), and connecting geographic patterns to morphological evolution, diversification, and extinction. Dommergues et al. (2001) explored relationships among Early Jurassic ammonoid morphologies and their geographic distribution and found a complicated pattern, with no clear relationship between morphotype and dispersal ability or environment. Navarro et al. (2005), on the other hand, were able to link the biogeography of Middle Jurassic cardioceratid ammonoids with morphological evolution. They found that immigration of ammonoids into new areas (tied to sea level rise) led to increased morphological disparity within the group while the subsequent invasion of a different clade led to a reduction in the first group's disparity. Yacobucci (2004b) found a similar result for Middle Cretaceous ammonoids from northern North America: invasion by a second ammonoid group into an endemic genus' geographic range resulted in a shift in the endemic ammonoid's morphology, presumably to avoid direct competition with the newcomer.

Jurassic-Cretaceous ammonoids displayed the expected latitudinal diversity gradient, with highest taxonomic diversity at low latitudes, decreasing towards higher latitudes (Cecca et al. 2005b; Yacobucci and MacKenzie 2007b; Vinarski et al. 2011; Rogov 2012). Cecca et al. (2005b) found that at a single latitude, ammonoid diversity was lowest on epicontinental platforms and higher in both intracratonic basins and deeper oceanic settings. Rogov (2012) argued that the latitudinal diversity gradient was a function of both temperature and the coming and going of ocean connections between basins as sea level fluctuated. Yacobucci and MacKenzie (2007b) similarly found that sea level rises in the Cenomanian and Campanian shifted peak diversities northward within the North American Western Interior Seaway, with the latitudinal gradient shifting back south in the intervening intervals (Fig. 8.5a). Also notable is the presence of an endemic center at mid-latitude within the Western Interior Seaway, where northern and southern faunas overlapped (Fig. 8.5b; Kauffman 1984). A variety of endemic ammonoid species and genera arose within this small region of the seaway.

The relationship between geographic range and rates of evolution and extinction has been explored for many marine animal groups (Jablonski 1986, 2005, 2008; Jablonski and Roy 2003; Payne and Finnegan 2007; Lockwood 2008; Janevski and Baumiller 2009; Myers et al. 2013; Nürnberg and Aberhan 2013). Large geographic ranges may decrease speciation rates (as Jablonski and Roy (2003) found for Cretaceous gastropods) while also providing protection from extinction (Jablonski 2008). Interestingly, Jablonski (2008) found that larger geographic ranges reduced extinction probability for bivalves, gastropods, and nautiloid cephalopods during the Cretaceous-Paleogene extinction but were of no help to ammonoid cephalopods; he argued that this difference resulted from some trait specific to ammonoids that increased the group's extinction probability.

8.5 A Synthetic View of Macroevolution and Paleobiogeography

8.5.1 A Synthetic Model for Ammonoid Speciation

Summarizing the key points made in this chapter, Jurassic-Cretaceous ammonoids show remarkable rates of diversification. Ammonoid diversity appears to be controlled by both "internal" biological processes, such as developmental flexibility, and "external" environmental factors that control habitat space and geographic distributions, including sea level cycles, tectonic shifts, oceanographic conditions, and climate change. Contemporary biological studies have shown that microallopatric, parapatric, and sympatric speciation are all viable alternatives to the traditional allopatric model, and that speciation may be driven by divergent natural selection to occupy different ecological niches. These processes may occur repeatedly in similar habitats, producing a pattern of parallel evolution like that frequently seen in J-K ammonoids.

Integrating these concepts and observations produces the following speciation model for ammonoids:

1. The ancestral ammonoid species moves into a new habitat, such as a newly formed epeiric seaway created by a sea level rise.
2. Small random changes in the flexible developmental program of individuals produce variable adult sizes and shell forms.
3. These variable morphs sort into different ecological niches and/or occupy distinct microhabitats within the epeiric seaway.
4. Assortative mating and disruptive selection result in reproductive isolation and divergence. If these subpopulations persist, one or more new, endemic species may be produced.
5. Finally, if a related ammonoid species later moves into a similar new epeiric habitat, it will undergo the same sort of process. Developmental constraints on shell form will result in the production of anatomical variants similar to earlier endemic radiations (i.e., homeomorphs), which will then sort themselves into similar microhabitats.

Note that under this model, speciation is implied to be sympatric or microallopatric. Different anatomical variants are produced in situ, and then separate out into microhabitats. These microhabitats may be patchily distributed within the same general region (e.g., different benthic substrates), or may result in a fossil record that combines multiple microhabitats in a single location (e.g., ammonoids occupying different portions of the water column). The model predicts that ammonoid morphology should match specific ecological niches consistently, that is, a particular mode of life is reflected in shell anatomy and size. The model also requires that the ecological niches to which ammonoid morphs adapt are consistently available through space and time.

This model of speciation emphasizes the importance of both biological processes (developmental flexibility) and environmental factors (sea level change and a mosaic of microhabitats) in explaining high diversification rates among ammonoids. Neither by itself is sufficient to explain ammonoid evolution. The inherent developmental flexibility of ammonoids can produce a great diversity of forms, but these will persist and diverge only when environmental conditions allow it. Sea level rises that produce new shallow marine habitat area may represent a particularly important environmental change driving ammonoid diversification. However, Holland (2012) documented that not all sea level rises are equal. While sea level rises necessarily increase the total area of flooded continent, they need not increase shallow marine habitat area, depending on what depth range of habitat one considers (e.g., 0–25 m, 75–100 m). Hence, a clade's response to sea level change will be contingent on the specifics of the case: what the starting sea level was, the particular bathymetric profile of that region, and the larger paleogeographic context. These subtleties may help to explain conflicting specific ammonoid case studies that show diversification peaks during transgressions vs. regressions, and a variety of complex relationships between macroevolution and paleobiogeography.

Testing this model for ammonoid speciation will require detailed interdisciplinary data for each radiating clade. A robust phylogenetic hypothesis of evolutionary relationships within the clade is an essential first step, as putative ancestor and descendent species must be identified. The extent of developmental flexibility in the ancestral lineage must be documented through investigation of morphological and ontogenetic variation within the group. Paleoecological, sedimentological, and geochemical data can demonstrate the existence of different microhabitats within a seaway, and the recurrence of similar microhabitats in different seaways. It is also critical to establish linkages between ammonoid shell form and size and specific modes of life or microhabitats within the clade. High resolution stratigraphic and geographic occurrence data will show whether the ancestral lineage existed outside the seaway before it formed and then moved into the seaway. Such data are also essential to demonstrate sympatry between ancestor and descendent lineages within the seaway and endemism of newly arising species.

A comparative approach may be the most effective way of testing this speciation model. An ideal test case would involve two co-occurring ammonoid clades, one of which shows rapid speciation and one of which does not. The speciation model presented here would predict that the diversifying clade will show a higher degree of developmental flexibility, more heterochrony, a greater number of endemic species, and more sympatry among species within the clade. A correlation between the opening of new shallow marine habitat space and pulses of diversification is also expected. These predictions could be tested if suitable clades can be identified for comparison.

8.5.2 New Directions in Studying Ammonoid Macroevolution

Given their rich fossil record and long history of study, Jurassic and Cretaceous ammonoids can serve as a model system for many areas of macroevolutionary investigation. Of utmost importance will be developing and testing phylogenetic hypotheses of relationship for J-K ammonoid clades. With this sound phylogenetic context, integrative work can proceed to investigate the relationships among diversification, morphospace occupation, geographic distribution, extinction, and environmental change. Such studies will be valuable at a variety of taxonomic, spatial, and temporal scales; detailed studies of individual clades will be complemented by global studies of ammonoid macroevolution across the entire Jurassic and Cretaceous Periods.

Sorely needed are comprehensive databases of J-K ammonoid occurrences. While the Paleobiology Database (PBDB; http://paleobiodb.org) has been used to investigate Cretaceous ammonoid paleobiogeography (Hendy 2009), it currently contains a limited number of ammonoid occurrences and its taxonomic coverage is incomplete. Various workers have developed their own ammonoid occurrence databases for particular regions and time intervals (e.g., Late Cretaceous Western Interior Seaway of North America database; Yacobucci and MacKenzie 2007a, b, 2008; MacKenzie and Yacobucci 2008). A priority for the field should be to integrate existing data sources into a single, open-access database of J-K ammonoid occurrences that is suitable for a range of quantitative and qualitative analyses.

Fossil occurrence data must be analyzed in the context of potential sampling biases. The PBDB team and others have developed a range of sampling standardization techniques that take into account variations in sampling intensity through time (Alroy et al. 2001, 2008; Alroy 2008, 2010; Kiessling 2008). Such techniques have not yet been tested on J-K ammonoids. Another potential bias is the availability of rock for sampling through time. Temporal and spatial variations in the amount of accessible outcrop are known to affect biodiversity patterns (Raup 1976; Peters and Foote 2001; Smith 2007; McGowan and Smith 2008), although whether outcrop map area or rock exposure area is a better metric is debated (Dunhill 2012). Of particular interest to ammonoid workers is the apparent correlation of marine invertebrate diversity to sea level cyclicity and the expansion and contraction of sedimentary basins (Smith et al. 2001; Peters 2005; Smith and McGowan 2005; Peters and Heim 2010, 2011; Hannisdal and Peters 2011). Such a pattern may demonstrate a significant sampling bias (Smith et al. 2001; Smith 2007; Wall et al. 2009) or may result from real biological processes that are associated with sea level change (the "common-cause" hypothesis; Peters 2005; Peters and Heim 2010, 2011; Hannisdal and Peters 2011). These competing options can be evaluated by detailed studies of J-K ammonoid occurrences. More generally, the completeness of the ammonoid fossil record could be assessed by estimating preservation rates (Foote 2003) or evaluating stratigraphic gaps implied by phylogenetic hypotheses (Wagner 2000). And, of course, taxonomic revisions of major J-K ammonoid groups are sorely needed in order to produce taxonomically standardized datasets.

Quantitative approaches to the integrative study of ammonoid evolution and biogeography have become more common over the last decade (Brayard et al. 2007; Hendy 2009; Dera et al. 2011; Brayard and Escarguel 2013; Brosse et al. 2013). Brayard et al. (2007) used a combination of approaches, including hierarchical cluster analysis, nonmetric multidimensional scaling, and their own nonhierarchical Bootstrapped Spanning Network technique to document paleobiogeographic patterns in the radiation of Early Triassic ammonoids after the Permo-Triassic extinction. Dera et al. (2011) used a similar quantitative toolkit to study ammonoid evolution through the Pliensbachian-Toarcian (Early Jurassic) interval. Such approaches should be expanded to later time intervals with more complex paleogeographic contexts.

Modern biogeographers are turning to the use of geographic information systems (GIS) and spatial statistics to document, quantify, and model biogeographic patterns and processes. Fewer paleontologists have made use of these tools, although they are a powerful method for investigating an array of questions, including reconstruction of geographic ranges, assessment of habitat tracking, and documenting the environmental drivers of evolution and extinction (Lieberman 2000; Stigall 2011; Yacobucci and MacKenzie 2007a, b, 2008; MacKenzie and Yacobucci 2008; Myers et al. 2013). As a comprehensive database for J-K ammonoids is constructed, we must be mindful of building spatial data into it so that it is fully compatible with GIS-based analyses.

A synthetic and quantitative approach to ammonoid macroevolution and paleobiogeography is necessary for us to understand the evolutionary dynamics of this most remarkable group of animals. As our database expands and new computational techniques are brought to bear on wide-ranging questions, J-K ammonoids will become a model for how marine animals evolve in a Greenhouse World.

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