

Chapter 10

Paleobiogeography of Late Cretaceous Ammonoids

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10.1 Introduction

Any attempt to synthesize the vast literature on Cretaceous ammonoids requires an acceptance of taxonomic identifications (and this comment is applicable to far more than our look here at Late Cretaceous ammonoid paleobiogeography). In the last century, there were paleontologists who mastered an understanding of ammonoid paleontology for entire Mesozoic periods, such as William J. Arkell and John H. Callomon for the Jurassic, and probably Leonard Frank Spath for the Cretaceous. In this young century, James W. Kennedy comes close to a global grasp of this enormous assemblage of regions and taxa. During the career of these and other researchers, the very diverse North Pacific Province and the Campanian and Maastrichtian of Antarctica were little known. Additionally, the exchange of literature and information was much more laborious than today.

Still, we faced challenges in the compilation of the data presented here: The information available for such a study is scattered, and many white areas remain on the maps. Another challenge in the compilation of the paleobiogeography of Late Cretaceous Ammonoidea is what can be called a “*monographic bias*”, i.e. that diversity is often related to the number of scientists and research effort aimed at a

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given region. Our task is further challenged by the fact that much of the history of ammonoid research has been driven by questions of biostratigraphy: what is the highest biostratigraphic resolution of Cretaceous strata that can be obtained? This has caused biostratigraphers to search for taxonomic units with the highest use, and thus, intraspecific variability of Late Cretaceous ammonoids was hardly studied, reducing the comparability of assemblages between regions and stratigraphic units. The many, highly ornamented Cretaceous ammonoids have perhaps more than any other group of fossils been affected by this.

Ammonoids have variable morphologies (De Baets et al. 2015; Monnet et al. 2015). More and more studies show that, when large numbers of specimens of ammonoids with variable ribbing, nodes, and other surface ornament, and to some extent even coiling geometry are looked at anew, many seeming species are found to be only variants. Blame cannot be attached here: this is how ammonoid systematic paleontology was done for a long time, and passed on from advisor to student. Examples abound, including the differentiation of the many “*species*” of the early Campanian *Submortonicerias* in California by Anderson (1958). Perhaps the most notorious splitter of those defining Cretaceous ammonoids was Thomel (1972) who defined 56 species and subspecies of which most are not more than variants of previously known species (for synonymies see, e.g., Wright and Kennedy 1984–1996). Examples are everywhere in Late Cretaceous ammonoid literature, and the challenge of the young generation of ammonoid taxonomists will be in reducing the vast number of species-names more than discovering valid new species.

Equally egregious, is a phenomenon which we call here the “*geographic bias*”. Quite often, ammonoids of the same species are given new names when found in different geographic regions. This phenomenon is quite pronounced among Cretaceous heteromorphic ammonoids. Because so many were unsuited for horizontal swimming of any efficiency (including turrilitids, most nostoceratids, ancyloceratids, diplomoceratids), when found in different countries, new names have routinely been given. This practice extended even to species of greatest biostratigraphic usefulness, with no case more egregious than in *Baculites*; Klinger and Kennedy (2001) listed more than 130 valid species names of *Baculites*. The work of William Cobban included the principle that the Late Cretaceous Western Interior was an endemic center, and among these were many species of *Baculites* unique to the Western Interior, or at most, ranging into the Gulf province of North America. Yet, new studies of *Baculites* from Antarctica show that North American *Baculites* species from there also occur in Antarctica, while some of our own work (still only published as abstracts: Ward et al. 2008, 2010; Ward 2009) has shown that, in fact, many of the Western Interior *Baculites* species are present on the West Coast of North America but with different names. Again, a challenge for the next generation of ammonoid specialists will be to reduce the nomenclature caused by this geographic bias, often compounded by preservation nature. The beautiful, aragonitic ammonoids from the Western Interior look quite different when they are found as molds in chalk facies of Denmark.

There has always been a wealth of data about Late Cretaceous ammonoid occurrences. This led to a series of interpretations of their paleobiogeography. A first

detailed approach was made by Reyment (1956) who discussed the affinities of Ammonoidea from Nigeria and Cameroon with those of North Africa, but without maps. An early example of a paleogeographic map with identification of provinces was given by Freund and Raab (1969) for the early Turonian. Jeletzky (1971) defined North American Cretaceous biogeographic units from both the Arctic and North Pacific provinces. A larger approach was made in the classic work of Matsumoto (1973) who plotted the distribution of abundant genera on geographic maps and thus defined and discussed thirteen provinces throughout the late Cretaceous. All these authors used paleobiogeographic terms like “*realm*” and “*province*” in differing senses. Paleobiogeographic terms are used here in the sense of Westermann (2000a, b) and Cecca (2002). In this nomenclature, superrealms are the largest biogeographic units, followed by realms and provinces. A biochore is a highly dynamic unit that not only expands and shrinks in range, but also changes in rank through time (Westermann 2000a): a realm can transform into a superrealm by increasing or into a province by decreasing its dominance and extent with time. In contrast to Page (1996), we recognize several realms: The Tethyan Realm, the Boreal Realm, the Arctic Realm and the Austral Realm.

By the Late Cretaceous, continuing continental movement opened an equatorial, Tethyan-distributional pathway that created a low latitude, globe spanning distributional pathway for ammonoids due to the onset of circumequatorial oceanic surface circulation (Skelton 2003). One result of this is that former barriers to migration disappeared to ammonoids and many other organisms, and this Tethyan corridor gave rise to a superrealm. At the same time, ammonoid distribution patterns demonstrate the existence of two other biogeographic units defined by ammonoids: the Arctic and Austral Realms of the high latitude northern and southern globe, respectively. The Pacific Realm spans both hemispheres and is intermediate between the Arctic and the Austral Realms. During the Late Cretaceous, the Pacific Realm began to differentiate into different ammonoid provinces, leading to the varying definitions of an Indopacific biogeographic Province, which was further differentiated by Jeletzky (1971) and Matsumoto (1971) into a North Pacific and a more tropical Indopacific Province. Combined, these can be called a Pacific Realm, but as we shall show below, near the end of the Cretaceous, an important differentiation took place creating even more biogeographic differentiation.

The Boreal and the Euramerican Realms were limited southwards by the Tethyan Realm. India was part of either the Austral or the Tethyan Realm, depending on prevalence of taxa (Westermann 2000b).

At the beginning of the Late Cretaceous, latitude was the main factor controlling ammonoid occurrences. Provincialism increased during the Late Cretaceous, which was related to the breakup of Gondwana by several authors (Macellari 1987; Bardhan et al. 2002). Endemism was distinct in epicontinental seas such as the Western Interior Seaway. The endemic evolution of Western Interior Seaway *Baculites* and *Scaphites* has been outlined in detail by Cobban (1993) and even more detailed by Kennedy and Cobban (1976). The Trans-Saharan Seaway was less stable and only occasionally connected the southern Tethyan shelf to the South Atlantic during the Cenomanian-Turonian and the Campanian-Maastrichtian transition

(Zaborski 1982; Courville et al. 1998). The Tethyan Realm decreased in importance due to the opening of the Atlantic, which established as a new province during the Late Cretaceous. On the continental shelf, provincialism was increasingly reduced due to the opening of migrational pathways. The hallmark of Late Cretaceous faunas was the virtually pandemic distribution of their genera and species (Page 1996) such as, e.g., *Diplomoceras*, *Pseudophyllites*, *Phyllopacchyceras*, or *Turrilites* (e.g. Kennedy and Cobban 1976).

10.2 Late Cretaceous Paleobiogeography

10.2.1 Cenomanian

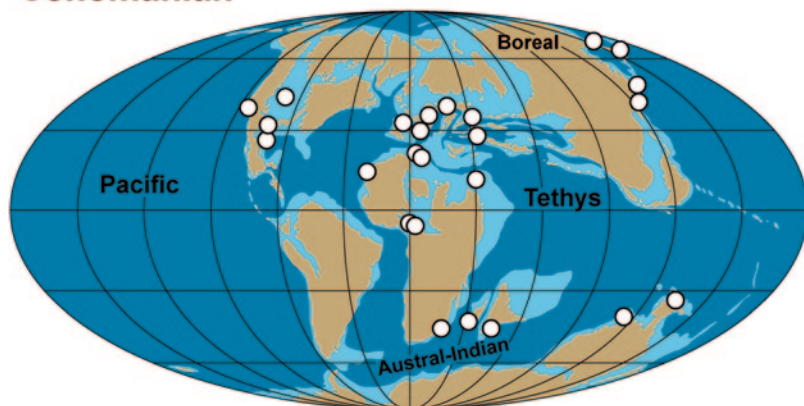
At the beginning of the Cenomanian, ammonoid faunas are characterized by endemic assemblages, e.g., well documented for the Boreal Realm by the Schloenbachiidae (including hoplitids, Cooper and Owen 2011) and for the western Pacific (Bando et al. 1987; Shigeta et al. 2010). With time, these faunas were invaded by radiating clades such as the Kossmaticeratidae and the Acanthoceratidae (Jagt-Yazykova 2011, 2012). Acanthoceratids derived from the Albian subfamily Stoliczkaiellinae (Kennedy et al. 2005b) and became a group with cosmopolitan occurrence, but they were always associated with endemic elements of the Acanthoceratidae and of other ammonoid families. The Arctic Realm was dominated by belemnites, and closely connected to the Boreal Realm (Page 1996). The Boreal Realm included Europe and reached as far as the northeastern limit of the Arabian platform during the early and middle Cenomanian (see summary in Monnet 2009).

During the Cenomanian, the main control on the distribution of the Ammonoidea became latitude, i.e. the Tethyan became a Superrealm, with the continents showing only little endemism. In the same stage, the Western Interior Seaway of the USA and Canada spread out from the North. Initially, it contained an endemic ammonoid fauna of Gastroplitinae such as *Neogastrolites* (Kennedy and Cobban 1976; Kauffman 1977; Hancock et al. 1993). When it finally opened to the South, Tethyan taxa entered the Western Interior Seaway, and it became a transitional route between the Arctic Sea and the Gulf of Mexico-central Atlantic.

In the middle Cenomanian, *Turrilites* for a short phase, achieved an almost global distribution in the Tethyan Superrealm (Fig. 10.1). At the middle-late Cenomanian transition, the genus disappeared, and the Turrilitidae became rarer and less dominant (Wright and Kennedy 1984–1996). In contrast, the Acanthoceratidae remained dominant elements, although there was a strong turnover at the generic level (summarized, e.g., in Monnet et al. 2003). At the same time, an increased faunal interchange in lower and middle latitudes was noted by Monnet (2009). The Collignoniceratinae and Vascoeratinae evolved, the latter being widespread in the southern Atlantic and Africa (Wright 1996).

During the latest Cenomanian, the faunas were stepwise reduced severely by the upcoming Oceanic Anoxic Event 2 (OAE 2) (e.g., Elder 1991; Monnet and Bu-

Cenomanian



○ *Turrilites costatus*

Fig. 10.1 The extension of the Tethyan Superrealm, exemplified by *Turrilites costatus* during the middle Cenomanian (Wright and Kennedy 1984–1996). Map based on 90 Ma reconstruction (Blakey 2002)

cher 2007), although several genera such as *Metoicoceras*, *Neocardioceras* or *Sciponoceras* still occupied the Tethyan Superrealm. Species longevity was shown to decrease during the Cenomanian (Monnet et al. 2003). Provincialism increasingly dominated the distribution of the remaining, more and more isolated species, e.g., in the Trans-Saharan Seaway (Courville et al. 1998; Courville 2007). In the same time, the last Turrilitidae occurred (Wright 1996). In latest Cenomanian sediments, ammonoids disappear from the fossil record, with very few exceptions preserved in sediments deposited in epicontinental seas such as the Western Interior Seaway and the Trans-Saharan Seaway (e.g., Cobban 1972; Kennedy and Cobban 1991; Courville et al. 1998).

10.2.2 Turonian

The distribution of the early Turonian ammonoids was dominated by the post-crisis radiation. By the beginning of the Turonian, provincialism was still not well defined: The realms were not well expressed, rather a subdivision into smaller provinces is noticeable (Freund and Raab 1969). The former realms re-established rapidly with the recovery from OAE 2 faunal crisis (Ifrim and Stinnesbeck 2007; 2008). Central Atlantic faunas differ from the rest of the Tethyan Realm (compare e.g., Kawabe 2003; Kennedy et al. 2005a; Ifrim and Stinnesbeck 2007; Nagm et al. 2010), but both are mixed in Brazil (Seeling and Bengtson 2002). This is the first clear expression of a new realm, the Atlantic Realm which is established more or less permanently from now on. In the western Pacific, faunas are composed of exclusively immigrating taxa (Jagt-Yazykova 2012). The Acanthoceratidae re-appeared and

rapidly became dominant faunal elements, but with taxa from the subfamily Euomphaloceratinae. With the dispersion of *Mammites nodosoides*, a global index for the middle early Turonian, the Tethyan Superrealm established again, expressed, e.g., in the widespread occurrence of the Mammitinae and the Collignoniceratinae from then on. At the same time, the Trans-Saharan Seaway contained a high percentage of endemic taxa, but a small part represents Tethyan species which used the co-occurring maximum of the global sea-level for immigration (Courville 2007).

In the middle Turonian, the Trans-Saharan Seaway disappeared (Courville et al. 1998). The Nostoceratidae and Polyptychoceratidae appeared (Wright 1996). Faunas from the northeastern Pacific show affinities with Japanese faunas (Haggart et al. 2005), although there, the faunas tend to show a high degree of endemism (Matsumoto 1977).

During the late Turonian, a cooling episode caused the short-term extension of the Boreal Realm southwards, indicated by a short phase of immigration of cool-climate faunas into Europe (Wiese and Voigt 2002). Endemism increased as reflected in strong provincialism, with only few ammonoid species showing wider occurrence (discussed e.g. in Walaszczyk et al. 2004); only some of the Barroisiceratinae reached a global distribution in lower and middle latitudes. The affinities between California, Alaska and Japan still existed (Haggart et al. 2005).

10.2.3 Coniacian–Santonian

At the beginning of the Coniacian, cosmopolitan ammonoids are rare, and endemic taxa dominated the faunas (compare e.g. Kennedy et al. 1995; Walaszczyk et al. 2004; Stinnesbeck et al. 2005). Few taxa, however, spread out over the Tethyan Superrealm, e.g. from the Barroisiceratinae or the Texanitinae. Their distribution seems to be limited by latitude alone, and their distribution is similar to that of *Turrilites* (Fig. 10.1). From the late Coniacian on, a fast succession of endemic heteromorphic species provides a biozonation with a high resolution in the Western Interior Seaway (Cobban et al. 2006).

Ammonoids from the Austral Realm comprise cosmopolitan genera such as *Gaudryceras*, *Kossmaticeras*, *Menuites*, *Nostoceras*, *Pseudophyllites* and *Tetragonites*. Most of the species of these genera were endemic (Kennedy et al. 2007).

The paleobiogeographic composition of ammonoid faunas during the Santonian is similar to that of the Coniacian, although the faunas underwent a worldwide change (compare Kennedy et al. 1995; Remin 2010; Jagt-Yazykova 2012). In some provinces, ammonoids were rare and little diverse, e.g., in the Boreal Realm (Kennedy and Kaplan 2000). During the Santonian, the number of endemic forms was at its Late Cretaceous maximum, indicating a strong provincialism (Kennedy and Cobban 1976). At the same time, a rich diversity of species among both ornamented and heteromorphic forms evolved, among them *Eubostrychoceras*, *Glyptoxoceras*, *Polyptychoceras*, *Ainoceras*, *Neocrioceras*, *Hyphantoceras*, and others (Matsumoto 1977; Ward and Mallory 1977). This diversity is as high as or higher than in most other Late Cretaceous ammonoid faunas.

10.2.4 Campanian

During the early Campanian, endemism continued to be widespread among Ammonoidea (Fig. 10.2), expressed by their moderate potential for long-distance correlation. It may, however, be that both taxonomic and geographic biases (noted in the introduction to this paper) have influenced the emergent paleogeographic picture. Across the Atlantic and Tethys, faunas between the northern and southern hemisphere were separated, with even the exchange between the continents of the northern hemisphere to some extent limited (see discussion in Ifrim et al. 2013). By contrast, the diverse ammonoid fauna from Antarctica shows some species common with the Indopacific and even North Pacific regions. This is reflected in the shared occurrences of *Eubostriochoceras*, *Ainoceras*, *Metaplacenticeras* or *Hoplitoplacenticeras* (Crame et al. 1991; Olivero 2007), among others, and indicates that a certain degree of faunal exchange between these vastly separate geographic areas existed across the Pacific Realm. In a similar fashion, Ward et al. (2008) showed the presence of *Baculites* and other heteromorphic ammonoids of the Western Interior on the Pacific coast, but having previously been given other names. For example, the important (but curiously never formally given a species name) *Baculites* sp. ‘smooth’, and its successive, *Baculites* sp. ‘weak flank ribs’ are common globally,

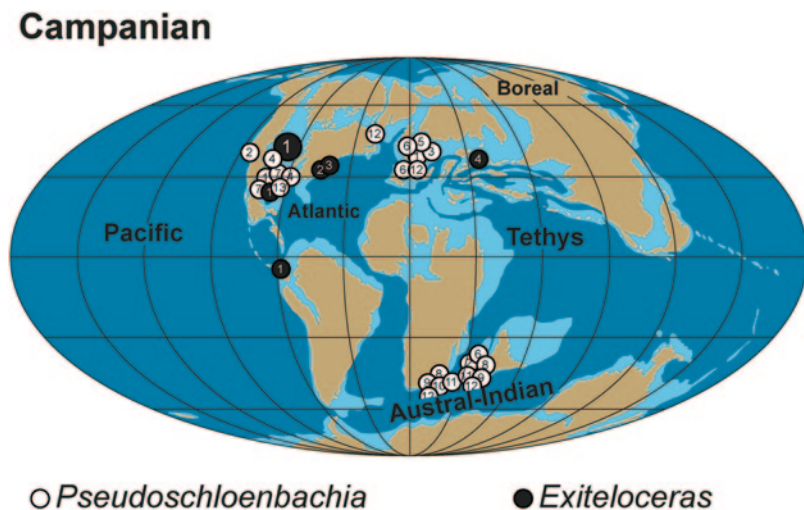


Fig. 10.2 Distribution of selected ammonoid genera during the Campanian: Distribution of *Pseudoschloenbachia*. 1 *P. bertrandi*, 2 *P. boulei*, 3 *P. casterasi*. 4 *P. chispaensis*. 5 *P. grossouvrei*. 6 *P. inconstans*, 7 *P. mexicana*, 8 *P. papillata*, 9 *P. spinosa*, 10 *P. subincisa*, 11 *P. trituberculata*, 12 *P. umbulazi*, 13 *P. wilsoni*. *Exiteloceras*: 1 *E. jenneyi*, 2 *E. oronense*, 3 *E. rude*, 4 *E. etequense*. Large dot: main distribution. The genera have a wide distribution, but at species level, provincialism is recognized. This pattern is applicable to many genera, although the biases described in the Introduction may play a role. Map based on 90 Ma reconstruction. (Blakey 2002)

with the name *B. inornatus* in the North Pacific. The same form is named *B. duharti* in South Africa, *B. sp.* in Europe, and is clearly global in its paleogeographic distribution (Ward et al. 2008, 2010; Ward 2009).

In the Western Interior Seaway, many new taxa did evolve (Myers et al. 2013), and it is currently accepted that few of these migrated into other realms; for example, *Scaphites hippocrepsis* appeared in the Atlantic and Boreal realms. However, the extreme preservational differences between the Boreal chalk-preserved faunas and the Western Interior has perhaps importantly obscured some relations.

In the middle Campanian, cosmopolitan genera, like *Pseudophyllites* and *Diplomoceras*, and subgenera, like *Nostoceras* (*Nostoceras*) and *Nostoceras* (*Bostrychoceras*), appeared and spread out over the world. These cosmopolitan taxa represent all orders of the Ammonoidea distinguished traditionally today (Wright 1996, although this subdivision was debated, e.g., by Engeser and Keupp 2002). This evolution and distribution of cosmopolitan taxa indicates an enhanced exchange between the hemispheres. Nevertheless, a considerable degree of provincialism was present to a certain degree everywhere.

In contrast, at the same time, there was a reduction, and finally complete removal of faunal exchange between Antarctica and the rest of the world. The Antarctic province showed the first and complete extinction of nostoceratids, scaphitids, baculitids, belemnites, and inoceramid bivalves, among others in the Late Campanian, millions of years before elsewhere in the world. A highly endemic fauna of largely kosmaticeratid ammonoids replaced this previous and largely cosmopolitan Antarctic ammonoid fauna (Olivero and Medina 2000; Olivero 2012). Some obstacle cut off the migration routes of ammonoids into, and out of Antarctica, and killed off two thirds of the fauna in the process.

10.2.5 Maastrichtian

Faunal provinces and realms were clearly expressed during the early Maastrichtian (Ifrim et al. 2004; Fig. 10.3); nevertheless, an exchange of taxa between the provinces was recognized and related to sea-level changes (Ifrim and Stinnesbeck 2010). By the end of the early Maastrichtian, a short cooling phase led to a mix of faunas from different latitudes and thus to a short appearance of Austral species in low latitudes (Ifrim et al. 2004).

During the early Maastrichtian, the northern connection of the Western Interior Seaway to the Arctic Sea was cut. Subsequently, this epicontinental sea disappeared at the beginning of the late Maastrichtian. At its final stage, it was inhabited entirely by specialized ammonoid taxa (Kennedy et al. 1998). At the same time, around the early-late Maastrichtian transition, nostoceratids became extinct (Goolaerts 2010).

The ammonoid diversity remained high during the late Maastrichtian, in some cases even higher than in the early Maastrichtian. This was first discovered for the sections in southwestern Europe and Antarctica (Ward 1990; Ward and Kennedy 1993) and later confirmed for eastern Russia (Jagt-Yazykova 2012), Tunisia

long, Paleozoic through Mesozoic range of the Ammonoidea, in fact this number is rarely exceeded among studies where a thorough and modern definition of ammonoid species has been made, for instance, where the submission of single species of highly ornamented and ornamentally variable species has been taken into account.

The traditional interpretation of a long-term decline was proven only for Japan: there was a constant decrease in ammonoid diversity since the early Campanian (Toshimizu et al. 2003). In many other regions, highly diverse ammonoid assemblages are documented to few meters to centimeters below the boundary, e.g., southwestern Europe (Ward 2009; Ward and Kennedy 1993), central Europe (Jagt 2002; Machalski 2005), eastern Russia (Jagt-Yazykova 2012), Tunisia (Goolaerts et al. 2004; Goolaerts 2010), the North American Atlantic coast (Landman et al. 2004a, b, c), Chile (Salazar et al. 2010), and Antarctica (Zinsmeister et al. 1989). An overview over the distribution of randomly selected ammonoid genera within the last few meters below the K/Pg is given in Fig. 10.4 (which also exemplifies the “*monographic bias*”). These last survivors are again from all four suborders. Some of them are from the conservative taxa that evolved during the Campanian. In addition, ecologically very resistant species evolved like *Hoploscaphites constrictus* (Machalski 2005; Salazar et al. 2010; Machalski et al. 2012), *Discoscaphites iris* (Landman et al. 2010, 2012), or *Sphenodiscus pleurisepta* (Ifrim and Stinnesbeck 2010; Landman et al. 2010). None of the last North American Ammonoidea belongs to the conservative taxa, which are present virtually anywhere else. Figure 10.4

Cretaceous/Paleogene boundary

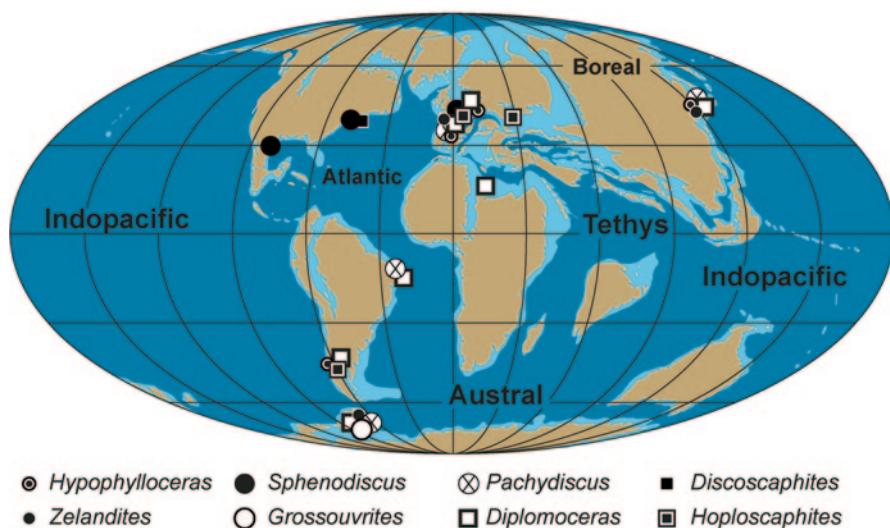


Fig. 10.4 Distribution of selected ammonoid genera at the Cretaceous–Paleogene boundary. The concentration of the taxa to defined bioregions is not recognizable anymore. (Map modified from 65 Ma reconstruction of Blakey 2002)

shows that the paleobiogeographic biochorema, which ruled Late Cretaceous biogeography until the late Maastrichtian, are not recognizable anymore at its end, with the exception of the long-term cut-off Austral Realm.

Occasionally, ammonoids are recorded from the earliest Paleogene, among them *Discoscaphites iris* and *Hoploscaphites constrictus* (Wiedmann 1988; Kennedy 1989, 1993; Birkelund 1993; Surlyk and Nielsen 1999; Machalski 2002, 2005; Machalski and Heinberg 2005; Landman et al. 2012), and most findings are clearly not reworked. These last representatives of the Ammonoidea occurred only in middle to high latitudes, but not in low latitudes (Stinnesbeck et al. 2012).

Conclusions

Despite (or because of?) the wealth of systematic descriptions, applications of quantitative approaches to ammonoid paleobiogeography are still lacking for the Late Cretaceous, but such are highly desirable. The qualitative interpretations given here are preliminary and need quantification using revised systematic and stratigraphic schemes.

The paleobiogeographic distribution of ammonoids was very dynamic throughout the Late Cretaceous. The strong endemism at the beginning of the Late Cretaceous was rapidly replaced by a Tethyan Superrealm. It broke down due to the crisis caused by the OAE 2 at the end of the Cenomanian but reestablished rapidly afterwards. During the Coniacian–Santonian, endemism increasingly ruled the distribution of ammonoids in the lower latitudes, with a peak in the early Campanian. In the late Campanian the interchange between the continents increased in the lower latitudes, whereas it was cut off in the Austral Realm. Genera and species which reach cosmopolitan distribution then appeared bit by bit. During the Maastrichtian, ammonoid diversity remained high, and realms and provinces were clearly expressed, although well connected. This provincialism broke down at the end of the Maastrichtian, when few ammonoids reached the K/Pg boundary and, in exceptional cases in middle and high latitudes, even crossed it.

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