Chapter 9
Paleobiogeography of Early Cretaceous Ammonoids

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9.1 Introduction

Ammonite dispersal is clearly related to paleogeographic patterns throughout the Mesozoic (Page 1996). Their distribution during life is thought to be controlled by physical barriers such as land masses and deep ocean basins, as well as by comprehensive environmental factors such as climate differences and oceanic circulation patterns (Kennedy and Cobban 1976; Cecca 2002; Cecca et al. 2005), while their biogeography is influenced by post-mortem transport along with other taphonomic and collection biases (Kennedy and Cobban 1976; De Baets et al. 2015; Naglik et al. 2015; Lukeneder 2015). Thus, a number of factors have an impact on their paleobiogeographic distribution.

The favored habitat of most ammonite families was the continental shelf (Westermann 1996), and these areas constantly changed as a result of fluctuating sea levels and plate tectonic movements on a large scale, particularly during the Early Cretaceous period (e.g. Föllmi 2012). Dynamic plate tectonic configurations that are strongly linked to sea-level changes trigger the migration of species

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by opening new migration routes (e.g. Wiedmann 1988). A prominent Early Cretaceous example of this is the opening of the Atlantic Ocean. Ammonite faunas from Brazil suggest that the opening of the central Atlantic created new migration routes as early as the Aptian, and the deepening of the young ocean, accompanied by deep-water circulation, was not established until the late Albian (Bengtson et al. 2007). Besides the impact of these physical barriers, ammonite dispersal in the Early Cretaceous is also believed to be temperature-related (Scott 1940; Michael 1979; Mutterlose 1992; Reboulet 2001). In recent decades, it has been assumed that temperatures were cooler in the earliest Cretaceous and rather moderate and warm from the Albian onwards, with less pronounced climate belts (e.g. Frakes et al. 1992). However, in the Berriasian-Aptian, and even after the onset of a warmhouse world in the late Early Cretaceous, it is a matter of debate whether temperature differences were more pronounced than was believed near the end of last century (Mutterlose et al. 2009; Erbacher et al. 2011; Papp and Cociuba 2013; Zakharov et al. 2013). Ammonites apparently were able to cope with drastic sea-surface temperature changes. The magnitude and frequency of temperature change during the Cretaceous, however, are still poorly constrained (e.g. Schouten et al. 2003, Dumitrescu et al. 2006), and the challenging question arises whether restricted ammonite distribution patterns are caused by climatic conditions or other factors (e.g. Kemper and Schmitz 1981; Marcinowski and Wiedmann 1988; Owen 1988a). Besides the significance of overall temperature differences in their habitats, it is even more important to understand the ammonite lifestyle and reproduction strategies to correctly interpret paleobiogeographic affinities. The latter factor is very rarely addressed with regard to ammonites in general (Manger et al. 1999; Mapes and Nützel 2009; reviewed in De Baets et al. 2015), but there has been some progress made in reconstructing the ammonite lifestyle in recent years (Ritterbush et al. 2014; Lukeneder 2015; Moriya 2015). But there is still much to be learned. A few recent studies actually use an integrated approach to address paleoenvironmental change and ammonite occurrence in great detail for the Early Cretaceous (e.g. Reboulet et al. 2005). These could answer some crucial basic questions on the background of paleogeographic distributions of Early Cretaceous ammonites, but there are still many problems to solve as well.

Differing taxonomic concepts often obscure ammonite distributional patterns (Kennedy and Cobban 1976; compare De Baets et al. 2015) and here we address many of the currently debated problematic issues. We distinguish biogeographic areas based on the distribution of ammonite taxa, as was performed in the pioneer work byNeumayr (1883). However, paleobiogeographic terms are updated to comply with Westermann (2000) and Cecca (2002). In this nomenclature, superrealms are the largest biogeographic areas. In contrast to Page (1996), we recognize a number of realms: The Boreal Realm, the Tethyan Realm, and the Austral Realm (for late Barremian to Albian times only). Occassionally, the additional distinctions of an Arctic (= A Sr; Berriasian-Hauterivian and Albian), a Boreal-Atlantic- (= B-A Sr; Berriasian-Aptian) and a Boreal-Pacific (= B-P Sr;Valanginian-? early Barremian) Subrealm as parts of the Boreal Realm are found to be reasonable. Similarly, a Mediterran-Caucasian (= MC Sr; Berriasian-Aptian) and an Indo-Pacific (= I-P Sr, Berriasian—early Barremian) Subrealm are distinguished as part of the Tethyan Realm.

Despite abundant systematic descriptions, quantitative approaches to ammonite paleobiogeography are still lacking for the Early Cretaceous. The qualitative interpretations given here are therefore an interim state of the art and need quantification in the future.

9.2 Early Cretaceous Paleobiogeography

9.2.1 Berriasian

In the early Berriasian, no Tethyan immigrants are found in the Boreal Realm and, conversely, there are no boreal species recorded from the Tethyan Realm (Rawson 1995a; Bulot 1996). This is one of the reasons why the definition of the Jurassic/Cretaceous boundary has been highly debated for many years and correlations between the Boreal and Tethyan realms are still at a preliminary stage (Wimbledon et al. 2011). In recent years, integrated magneto- and biostratigraphy have allowed a better correlation between the two realms, and it is now generally accepted that the latest Volgian correlates with the earliest Berriasian (Zakharov and Rogov 2008; Wimbledon et al. 2011, 2013; Bragin et al. 2013; Rogov 2013). As a consequence, it is now clear that the Jurassic/Cretaceous boundary is not marked by a significant ammonite turnover above the suprageneric level, neither for the Boreal nor Tethyan realms (Tavera et al. 1986; Zakharov et al. 1996; Rogov 2013).

There is a clear difference between the Tethyan record and that of the Boreal Realm, underlining the distinction between these faunal realms (Fig. 9.1). In the Boreal Realm members of the family Polyptychitidae dominate the record, particularly *Craspedites, Praetollia* and *Chetaites* (Baraboshkin 2002; Zakharov and Rogov 2008).

In the earliest Berriasian, the Tethyan Realm ammonite faunas are more diverse than those of the Boreal Realm, and are dominated by ammonites of the family Neocomitidae. The distributions of *Berriasella, Pseudosubplanites, Malbosiceras, Delphinella, Dalmasiceras, Strambergella* and *Pseudoneocomites* are restricted to the Mediterran-Caucasian Subrealm (Le Hégarat 1973; Kotetishvili 1988; Wimbledon et al. 2013). Earliest Berriasian *Berriasella s. str.* are only known from southern and central Europe, North Africa, Ukraine, the Caucasus and northern Iran (unpublished data), in contrast to a much wider geographic distribution often attributed in recent decades (Fig. 9.1) due to a more casual definition of this genus.

A most interesting change in the ammonite distribution occurs during the (?) late early to early late Berriasian. The Boreal Realm is characterized by the decline of the Craspeditinae and Dorsoplanitinae and the diversification of the Tolliinae (Baraboshkin 1999). The Arctic and Boreal-Atlantic subrealms both exhibit

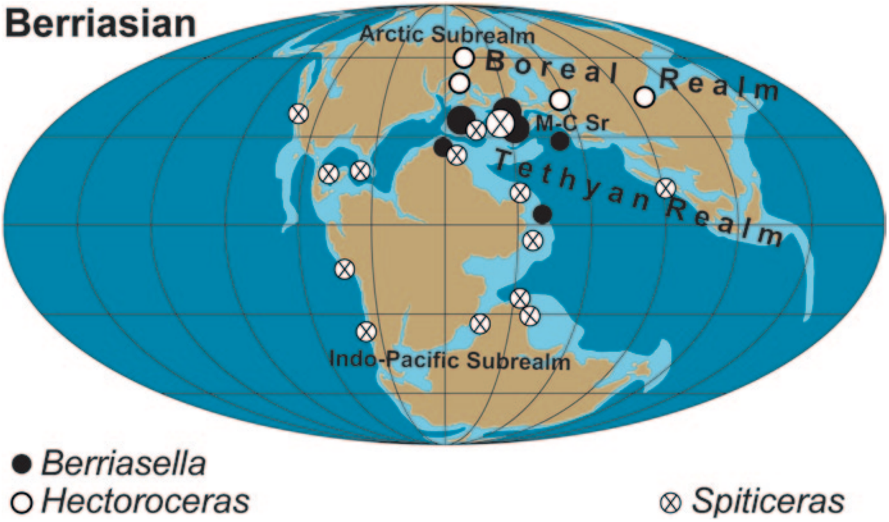

Fig. 9.1 Aspects of Berriasian ammonite paleobiogeography. Map based on 150 Ma reconstruction (paleomaps after Ronald Blakey, http://cpgeosystems.com/index.html, accessed 6th of June 2014). Larger dots indicate the home range and peak occurrence of a genus if it is more widely distributed. *M-C Sr* Mediterran-Caucasian Subrealm of the Tethyan Realm

the occurrence of *Hectoroceras* (Casey 1973; Birkelund et al. 1983; Baraboshkin 1999; Fig. 9.1). Among the Tolliinae, *Surites* is widely distributed in the late Berriasian of the Boreal Realm (Shul'gina 1985, 1989; Zakharov et al. 1996). According to Baraboshkin (1999), two areas of diversification of the Tolliinae can be distinguished that roughly correspond to the Arctic and Boreal-Atlantic subrealms. It should also be noted that the Eastern European part of the Boreal Atlantic Subprovince contains Tethyan genera that are also known from the eastern part of the Mediterran-Caucasian Subrealm, such as *Riasanites* and *Transcaspiites* (Mitta 2007, 2011).

Ongoing research (unpublished data) suggests that the affinities of the ammonites of Tethyan origin from the Polish Lowland and Russian Platform are even stronger with the fauna of Crimea, the Caucasus and Mangyshlak described by Luppov et al. (1988), Kvantaliani (1999) and Arkadiev et al. (2012). Assemblages of the eastern part of the Mediterran-Caucasian Subrealm (Caucasian and Transcaspian areas) are dominated by endemic Neocomitidae such as *Tauricoceras* and *Gechiceras*. Other important elements of the assemblage are *Euthymiceras* and *Hegaratia* (= *Balkites*), which are only known from a limited number of specimens in the western part of the Mediterran-Caucasian Subrealm (Le Hégarat 1973; Patrulius and Avram 1976). In contrast, the equivalent faunas from the western part of the Mediterran-Caucasian Subrealm are dominated by *Berriasella, Mazenoticeras, Tirnovella, Fauriella* and *Jabronella*.

Because of correlation problems (e.g. Zakharov et al. 1996), the limits of the Berriasian stage outside the areas discussed above are poorly understood. The marked endemism discussed above also affects the Indo-Pacific Subrealm. In Argentina and Chile, the faunas are dominated by *Andiceras*, *Argentiniceras*, *Frenguelliceras*, *Hemispiticeras*, *Cuyaniceras* and *Pseudoblanfordia* (Riccardi 1988; Aguirre-Urreta et al. 2007a; Parent et al. 2011; Vennari et al. 2012). Similarly, the endemic *Kossmatia*, *Durangites* and *Substeueroceras* assemblage of Mexico is now considered as Berriasian (Olóriz et al. 1999).

The conspecificity of the Berriasian ammonites described by Collignon (1962) from Madagascar with Mediterran-Caucasian taxa is still unsolved, at least regarding *Berriasella* (unpublished data). In our opinion *Subthurmannia* from Pakistan (Spath 1939; Fatmi 1977) are fully distinct from *Fauriella* of the Mediterran-Caucasian Subrealm (Bulot 1995).

Our ongoing research suggests that the endemism of the Neocomitidae at the genus level during the Berriasian is much higher than it has been previously assumed in the literature, and that homeomorphy (see Monnet et al. 2015) has led to erroneous taxonomic interpretations.

In our current stage of understanding, *Spiticeras*, and early Olcostephanidae originally described from the Himalayas are the only taxa spread throughout the Tethyan Realm. This links the Mediterran-Caucasian and Indo-Pacific subrealms, with populations reported from the Pacific Coast of America (Jeletzky 1965; Imlay and Jones 1970), Madagascar (Collignon 1962) and the shelf basins of South America and Antartica (Thomson 1979; Riccardi 1988; Aguirre-Urreta et al. 2007a; Parent et al. 2011).

9.2.2 Valanginian

As already outlined by Rawson (1981), Shul'gina et al. (1994), Baraboshkin (1999) and Alsen (2006), the paleobiogeographic patterns of the early Valanginian are almost identical to the late Berriasian. The faunas of the Boreal Realm are dominated by the Tolliinae and their derivatives the Polyptychitinae, while the Tethyan are still characterized by the abundance of the Neocomitidae (Kotetishvili 1983). The distribution of ammonites in the Boreal Realm is complex, partly due to the individual flooding history of former mainlands, and was discussed in great details by Jeletzky and Kemper (1988), Shul'gina et al. (1994), Baraboshkin (1999) and Alsen (2006).

A striking feature is the emergence and radiation of the Platylenticeratinae in the Boreal-Atlantic Subrealm. *Platylenticeras* characterizes the earliest marine beds resting on the continental Early Cretaceous (Wealden facies) in North Germany (Kemper 1961; Kemper et al. 1981; Elstner and Mutterlose 1996). Although there are conflicting opinions in the literature today (Bulot 1996), the idea that *Platylenticeras* is a neocomitid with a Tethyan origin is now favoured (see discussions in Alsen and Rawson 2005). At any rate, in Germany, *Platylenticeras* developed a high diversity (Kemper 1961, 1992; Hoedemaeker 2012 refers to drift occurrences, probably originating from Germany). This is in contrast to other European countries, from which only a limited number of species are known and where it is rare (Baumberger 1908, 1928; Thieuloy 1977; Vašíček 1979, 1997). In Greenland, and simultaneously on the Russian plate, *Delphinites* (*Pseudogarnieria*) faunas developed, ammonites belonging to the same subfamily Platylenticeratinae (Alsen and Rawson 2005). *Delphinites* (*Pseudogarnieria*) emphasize the very endemic character of early Valanginian ammonite faunas in the Boreal Realm, as in *Platylenticeras* there is a number of regionally occuring species only.

A transgression in the middle part of the early Valanginian wiped out these strong differences of the earliest Valanginian, and Polyptychitinae replaced the platylenticeratid faunas in the Boreal-Atlantic Subrealm (Jeletzky and Kemper 1988; Rawson 1981, 1993, 1994; Alsen 2006).

In contrast, the earliest Valanginian assemblages of the Tethyan Realm are dominated by neocomitids; the most prominently recorded genera are *Neocomites*, *Kilianella*, *Sarasinella* and *Thurmanniceras* (Rawson 1981; Kotetishvili 1983; Company 1987). Except for *Sarasinella*, these genera were originally defined based on species originating from the western part of the Mediterran-Caucasian Subrealm. There is no consensus on the definitions and the paleogeographic distributions of *Thurmanniceras*, *Sarasinella* and *Neocomites*. This problem has been addressed often in the literature (Company 1987; Bulot 1995; Aguirre-Urreta and Rawson 1999; Ettachfini 2004; Rawson 2007; Aguirre-Urreta et al. 2008). According to our current stage of knowledge, *Kilianella* is the only neocomitid that had a widespread distribution over the Mediterran-Caucasian and Indo-Pacific Subrealms of the Tethyan Realm.

Most interesting is the development of a very peculiar earliest Valanginian assemblage dominated by *Lissonia* and its potential macroconch *Raimondiceras* in South American basins of the Indo-Pacific Subrealm (Lisson 1907; Haas 1960; Leanza 1972; Etayo-Serna 1985; Mourgues 2004; Aguirre-Urreta et al. 2007a). As already pointed out by Aguirre-Urreta and Rawson (1999) and Aguirre-Urreta et al. (2008), these forms most likely evolved from the earliest Valanginian endemic Neocomitidae. Poorly constrained early Valanginian faunas were also reported from the Pacific coast of North America, where a mixture of endemic Neocomitidae (*Paskentites*, alleged '*Kilianella*' and '*Thurmanniceras*' as well as '*Sarasinella*' *sensu lato*) and Tolliinae (*Tollia*, *Neocraspedites*) were described by Imlay (1960) and Imlay and Jones (1970).

The continuous significant sea level rise that marks the Lower/Upper Valanginian boundary interval (see discussion in Föllmi 2012) led to an enhanced exchange of genera in the wider transitional zone between the Tethyan and the Boreal Realms in Europe (Kemper et al. 1981; Rawson 1993; Bulot 1993, 1996; Föllmi 2012). At this time a group of six Tethyan immigrant genera appeared, even in the fairly isolated epicontinental basins of North Germany, northeastern England and Poland (Kemper et al. 1981; Kutek et al. 1989; Kemper 1992; Kutek and Marcinowski 1996).

Some of these taxa, including *Olcostephanus* (Fig. 9.2)*, Karakashiceras*, and *Neohoploceras,* originated in the central part of the Mediterran-Caucasian Subrealm, but were dispersed as a result of this event not only to the Boreal-Atlantic Subrealm, but also over most of the Indo-Pacific Subrealm. This assemblage is well documented in Pakistan, Madagascar and South Africa (Bulot, 1990), Central

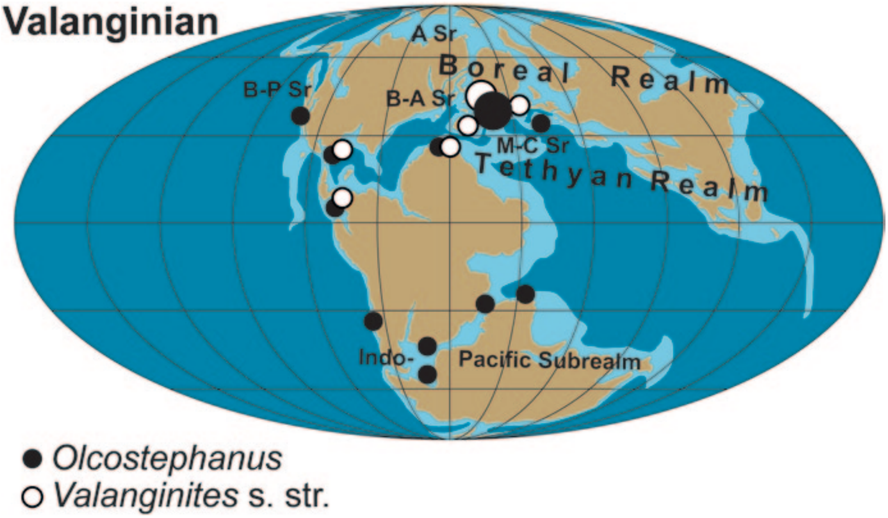

Fig. 9.2 Aspects of Valanginian ammonite paleobiogeography. Map based on 150 Ma reconstruction. *B-A Sr* Boreal-Atlantic Subrealm, *B-P Sr* Boreal-Pacific Subrealm, *A Sr* Arctic Subrealm, all of these are subrealms of the Boreal Realm. For further details see caption to Fig. 9.1

America (Etayo-Serna 1985; Young 1988; González-Arreola 2007) and the Andean Basins of South America (Rawson 2007; Aguirre-Urreta et al. 2007a, 2008). During that time *Olcostephanus* even reached the Pacific coast of North America (Imlay and Jones 1970) and Antartica (Howlett 1986).

In contrast, the worldwide distribution of the cadicone *Valanginites* appears doubtful. South American occurrences are clearly dated from the earliest Valanginian (see discussion in Aguirre-Urreta et al. 2008), whereas in the Mediterranean areas the stratigraphic distribution of *Valanginites* is well dated from the late early and early late Valanginian (Bulot et al. 1990). Aguirre-Urreta et al. (2008) claim that the South American *Valanginites* gave rise to the Mediterranean ones. In our opinion this view is open to discussion, and we favor the idea that *Valanginites* is paraphyletic and that two distinct lineages evolved from the *Olcostephanus* rootstocks at different times. We therefore indicate the distribution of *Valanginites* s. str. herein, contrasting a global distribution that is often attributed to this genus (Fig. 9.2). Dzik's (1990) interpretation of *Valanginites* as a macroconch of the small, spine-bearing *Saynoceras* refers to earliest Valanginian forms, but in addition to distinct shell features, the comparatively restricted paleobiogeographic distribution of *Saynoceras* compared to *Valanginites* argues against an interpretation as a dimorphic pair (see Ploch 2003, 2007 for an alternative interpretation).

In the Boreal Realm, the late early to early late Valanginian is marked by the rapid evolution of Polyptychitinae rising from the Polyptychitinae rootstock, and this radiation gave rise to new genera (*Hollwediceras*, *Prodichotomites*, *Dichotomites*, *Homolsomites*, *Ringnesiceras*, *Amundiptychites*) in the epicontinental basins of the Boreal-Atlantic, Boreal-Pacific and Arctic subrealms (Kemper 1978; Jeletzky and

Kemper 1988). The timing and phylogenetic relationships among those taxa remain largely unclear. Nevertheless, *Hollwediceras*, *Prodichotomites* and *Dichotomites* are known from scattered occurrences along the northern margin of the Mediterran-Caucasian Subrealm from Mangyshlak to southeastern France (Thieuloy 1977; Luppov et al. 1983; Thieuloy et al. 1990; Kuhn 1996; Reboulet 1996; Vašíček and Michalík 1999; Dziadzio et al. 2004; Lukeneder 2004).

Characterization of the latest Valanginian paleobiogeography in the Boreal Realm is difficult. It is generally accepted that *Homolsomites* and its junior subjective synonym *Wellsia,* dominate ammonite assemblages of the northern Boreal Realm, the Boreal-Pacific- and Arctic Subrealm of this time interval (Shul'gina et al. 1994; Wright et al. 1996; Baraboshkin 1999; Alsen 2006). Furthermore, successive pulses of Tethyan ammonite migrations from the Mediterran-Caucasian Subrealm characterize the latest Valanginian successions of the Boreal-Atlantic Subrealm, especially with regard to North Germany (Kemper et al. 1981; Kemper 1992; Rawson 1993). These progressive migrations peaked in the latest Valanginian with an ammonite assemblage almost entirely composed of Tethyan (*Olcostephanus*, '*Eleniceras*', *Teschenites*) or Tethyan derived (*Stoicoceras*) ammonites (Quensel 1988).

In the Tethyan Realm, the latest Valanginian is poorly documented outside the Mediterranean regions and Argentina. Recent investigations clearly show a strong endemism during this time interval in the Andean basins of the Indo-Pacific Subrealm with faunas dominated by endemic Neocomitidae (*Pseudofavrella*, *Chacantuceras*, *Decliveites*) (Aguirre Urreta and Rawson 2003, 2010). Outside Argentina, *Pseudofavrella* may be represented in Colombia (Etayo-Serna 1985), but the age of these Valanginian forms, which occur above the early Valanginian *Lissonia* fauna is very poorly constrained.

9.2.3 Hauterivian

The earliest Hauterivian is characterized by a radiation of the Neocomitidae (Ivanov and Aristov 1969; Baraboshkin 2002, with references; Baraboshkin et al. 2003; Alsen 2006). This excludes the Arctic Subrealm and the eastern part of the Boreal-Atlantic Subrealm, where impoverished polyptychitid faunas (*Homolsomites*, *Pavlovites*, *Subspeetoniceras* and *Gorodzovia*) occur. In the western part of the Boreal-Atlantic Subrealm, this faunal change is marked by the appearance of *Endemoceras*, a typical Tethyan-derived neocomitid (Kemper and Wiedenroth 1987; Rawson 1995a). The regularly coiled *Endemoceras*, a genus yielding important index species, progressed into the heteromorphic descendant *Distoloceras* (Kemper et al. 1981; Rawson 1993). *Distoloceras* is strictly restricted to the earliest Hauterivian of northern Europe, and the report of the genus from the late Valanginian is based on the misinterpretation of homeomorphic neocomitids that belong to *Rodighieroites* (Company 1987; Bulot 1995; Barragán and González-Arreola 2009). Interestingly, *Distoloceras* is a homeomorph (compare Monnet et al. 2015 for its definition) of crioceratids of Tethyan origin, with spines and a loosely coiled spiral (Kemper and Wiedenroth 1987).

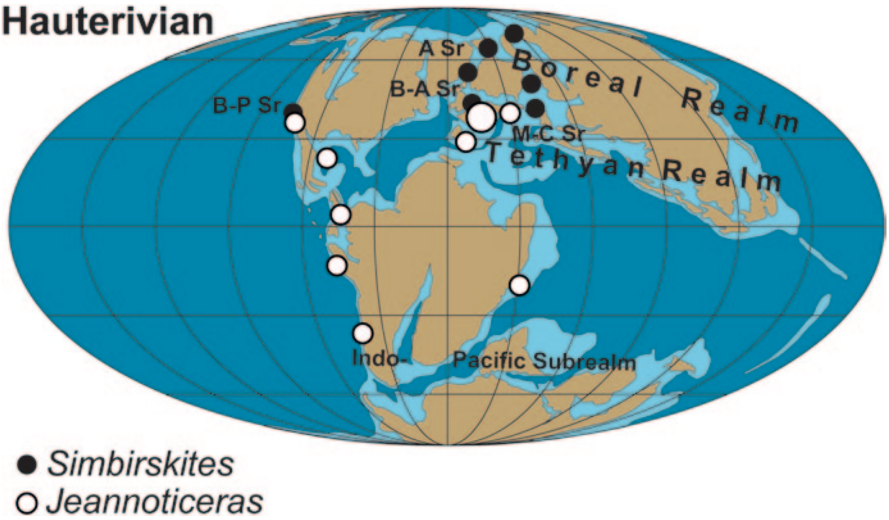

Fig. 9.3 Aspects of Hauterivian ammonite paleobiogeography. Map based on 120 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Acanthodiscus, *Leopoldia* and *Breistrofferella* are rare elements of the western Boreal-Atlantic ammonite faunas (Kemper 1992; Bulot 1995; Rawson 1995a). These genera provide a very useful link between the Boreal and Tethyan realms during the early Hauterivian. The paleogeographic distribution of *Acanthodiscus* and *Leopoldia* is facies-controlled and centered on the shelves of the northern margin of the Mediterran-Caucasian Subrealm (France, Switzerland, Ukraine), although a single occurrence is known from Morocco (Wippich 2001; Ettachfini 2004). As in the case of *Distoloceras*, reported occurrences of *Acanthodiscus* and *Leopoldia* in the late Valanginian are based on misidentified homeomorphic genera, including *Neohoploceras, Karakashiceras, Chacantuceras* and *Pseudofavrella* (Company 1987; Bulot 1995; Reboulet 1996; Aguirre-Urreta and Rawson 1999, 2010). Nevertheless, earliest Hauterivian faunas are poorly documented in the Indo-Pacific Subrealm except for the Neuquén Basin of Argentina, where the fauna is almost exclusively composed of *Holcoptychites*, an endemic member of the Spiticeratinae (Aguirre-Urreta and Rawson 2003; Aguirre-Urreta et al. 2008). The *Favrella* fauna of Patagonia and Antarctica is also an endemic development, but its early Hauterivian age needs final proof (Aguirre-Urreta et al. 2007a).

A major Hauterivian ammonite event is seen in the widespread distribution of the short-lived olcostephanid *Jeannoticeras* and associated *Olcostephanus* species that is well documented from the Boreal-Atlantic, Mediterran-Caucasian and Indo-Pacific subrealms (Bulot 1990; Bulot et al. 1993; Aguirre-Urreta and Rawson 2001) in the middle part of the early Hauterivian (Fig. 9.3). This appearance marks the onset of the mid-Hauterivian episode according to Rawson (1993, 1994). In the western part of the Mediterran-Caucasian Subrealm the neocomitids vanished progressively in the early Hauterivian and were replaced by *Crioceratites, Spitidiscus* and late

Olcostephanus (Rawson 1993). The paleobiogeographic development of neocomitids is made even more complex by the disappearance of *Endemoceras* in England, which is followed by a substantial re-appearance of *Lyticoceras* in France, with the latter probably evolved from the latest *Endemoceras* species (Kemper et al. 1981; Rawson 1993). Another highly significant ammonite faunal turnover for this stratigraphic interval is marked by the replacement of *Endemoceras* in the western limits of the Boreal-Atlantic Subrealm by *Simbirskites* that evolved in the Arctic Subrealm during the earliest Hauterivian (Rawson 1994; Baraboshkin 2002; Baraboshkin et al. 2003; Fig. 9.3). The mid-Hauterivian faunal change also strongly triggered the development of heteromorphic ammonites, which spread into the Boreal-Atlantic-, Boreal-Pacific- and Indo-Pacific Subrealm (Immel 1978, 1979a, b; Rawson 1993, 2007; Baraboshkin 2002; Aguirre-Urreta et al. 2008).

Generally, in the late Hauterivian, heteromorphs become increasingly important and dominate the ammonite assemblages of the Tethyan Realm while the Boreal Realm faunas are dominated by *Simbirskites* (Rawson 1994; Baraboshkin 2002). Whereas *Simbirskites* is absent from the western part of the Mediterran-Caucasian Subrealm, this genus represents a significant element in the Transcaspian area (Kakabadzé 1983; Kemper and Wiedenroth 1987; Baraboshkin 2002). Following the decline and extinction of the Olcostephanidae, Neocomitidae and Leopoldidae, new families appeared or flourished in the Mediterran-Caucasian Subrealm, such as the Abrytusitidae (*Spitidiscus*), Pulchellidae (*Subsaynella, Discoidellia*) and Barremitidae (*Plesiospitidiscus*), which reached the Andean basins of the Indo-Pacific Subrealm in the early late Hauterivian (Vermeulen 2002, 2005, 2007; Vermeulen and Bulot 2007; Rawson 2007; Aguirre-Urreta et al. 2008). In the latest Hauterivian, the recoiling of crioceratids brings rise to *Pseudothurmannia* (Wiedmann 1969) and allied genera/subgenera as important index species in the Western Tethys (Cecca et al. 1998; Company et al. 2003; Vermeulen et al. 2009; Hoedemaeker 2013).

Late Hauterivian successions of the Indo-Pacific Subrealm are as poorly known as those of the early Hauterivian. Re-examination of *Menuthiocrioceras* and *Malgasaynella* has showed us that these genera are of late Barremian age (see below) and thus Collignon's (1948, 1962) record of late Hauterivian in Madagascar and Indonesia is incorrect. In contrast, late Hauterivian strata are well developed in the Andean basins of Argentina and Chile (Aguirre-Urreta et al. 2007a). Although relationsships of the Andean basins to the Mediterran-Caucasian Subrealm have been known for quite a long time, a strong endemism was assumed by Leanza and Wiedmann (1980). This is relativized today because diversity in this area is higher than previously believed (Aguirre-Urreta et al. 2007a, b). The most striking feature of the faunas is the presence of local heteromorphs that evolved from Tethyan-derived *Crioceratites.* Identification of *Hemihoplites* from the Hauterivian of Patagonia (Riccardi and Aguirre-Urreta 1989; Aguirre-Urreta 2002) is questionable, since the evolution of *Hemihoplites* in the late Barremian of southeastern France has now been well established (Bert et al. 2006, 2008) and the Patagonian species show only superficial morphological similarities with the Mediterranean taxa. An *Aegocrioceras* species reported from Chile (Aguirre-Urreta et al. 2007b) is most likely a local offshoot of the Tethyan-derived *Crioceratites* of the *schlagintweiti* group rather than indicating paleobiogeographic affinities to the European Boreal Realm.

9.2.4 Barremian

The sea-level lowstand initiated in the late Hauterivian, and marking the early Barremian, is believed to be responsible for an increasing diversity in ammonite faunas, as individual basins became isolated (Rawson 1993). The Barremian was marked by the prevalence of continental conditions over most of the Arctic Subrealm (Jeletzky 1970; Rawson 1981; Baraboshkin 2002 with references) while carbonate platforms developed on both margins of the Mediterran-Causasian Subrealm (Philip 2003 with references). The key feature of the Barremian ammonite faunas is the development of rich faunas with heteromorphic ammonites.

Boreal Barremian ammonite faunas are known from the United Kingdom and Germany only, thus representing a comparatively small area of this realm. In the earliest Barremian of the Boreal Realm, the last occurrence of *Craspedodiscus* is remarkable, since it represents the last subgenus of the major Boreal ammonoid clade of the family Polyptychitidae (Rawson 1971, 1981). It is worth noting that the reported occurrence of *Simbirskites* (*Milanowskia*) sp. from the early Barremian of Japan (Matsukawa 1988) is highly doubtful and based on poorly preserved specimens that superficially match Hauterivian simbirskitids. As a consequence, the migration of Boreal ammonites in the Tethyan-dominated assemblages of the Far-East terranes of Asia is not substantiated.

Boreal-Atlantic shelf deposits are characterized solely by Tethyan and/or Tethyan-derived heteromorphs after the extinction of simbirskitids. The systematic treatment of these heteromorphs varies from one author to another. The most frequently cited genus is *Paracrioceras*. It is considered to be a senior subjective synonym of *Emericiceras* by Rawson (1975) and Wright et al. (1996), a view that is rejected by Vermeulen (2004, 2006) and Kakabadzé and Hoedemaeker (2010), albeit for different reasons. By contrast, Wiedmann (1962) and Immel (1978) regarded *Paracrioceras* as a synonym of *Crioceratites*. Thus *Crioceratites*, *Paracrioceras* and *Emericiceras* are defined inconsistently and reflect the poor state of early Barremian heteromorph taxonomy, which is confusing. The problem was also addressed by Klinger & Kennedy (1992) and Kakabadzé & Hoedemaeker (2004) when discussing the systematic assignment of South African and South American faunas. In our opinion, *Crioceratites*, *Emericiceras* and *Paracrioceras* are unsuitable to define paleobiogeographic groupings in the Barremian. As a consequence they are of little help to define the limits of paleobiogeographic units.

Therefore, the limits of distribution of normally coiled ammonites occuring in the Tethyan Realm, excluding heteromorphs, is extremely important in drawing the southern boundary of the Boreal Realm (Hoedemaeker 1990), particularly since they do not occur in the Boreal Realm (Rawson (1993, (1994). Among others, the earliest to early late Barremian Holcodiscidae (*Holcodiscus*, *Parasaynoceras*), Pulchelliidae (*Pulchellia*, *Nicklesia, Heinzia*) and Barremitidae are widely distributed from Japan to northern South America (Mexico, Colombia). Along the Pacific coast, spot occurrences of Pulchellidae extend as far north as California (Murphy 1975) and as far south as northern Chile (Aguirre-Urreta et al. 2007a) where they are associated with a fairly diverse assemblage of heteromorphs including the

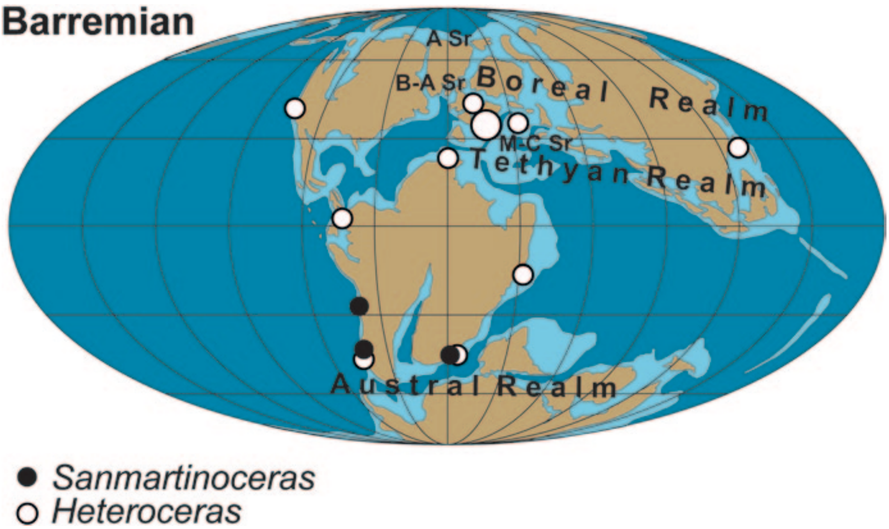

Fig. 9.4 Aspects of Barremian ammonite paleobiogeography. Map based on 120 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Circum-Pacific genus *Shasticrioceras*, which is also known from Arctic Canada (Jeletzky 1970) and Japan (Matsukawa and Obata 1993).

In the Mediterran-Caucasian Subrealm, the late Barremian is marked by a drastic change in the evolution of the ammonite faunas. Holcodiscidae and Pulchellidae have dissappeared and heteromorphs are highly diverse (Vermeulen 2005; Bert et al. 2008). Among heteromorphs the Hemihoplitidae and Heteroceratidae show the most striking morphological changes; the former are characterized by a recoiling of the shell, and the latter by the development of a helicoidally coiled inner whorls (the global distribution of *Heteroceras* is shown in Fig. 9.4). Both families provide faunal links with the Boreal-Atlantic Subrealm, since *Spinocrioceras* has been reported from Germany (Kemper 1973, 1995) and *Heteroceras* from the United Kingdom (Rawson 1995b).

Although imperfectly dated, the onset of the Austral Realm, centered on Patagonia, Australia, Africa and Madagascar, most likely took place in the late early to early late Barremian. Non-heteromorphic ammonites endemic to this area includes *Hatchericeras*, which stands among the candidates for the last representative of the Perisphinctoidea, even though its last occurrence is not accurately dated with respect to the Simbirskitinae (Riccardi 1988; Kennedy and Klinger 1990). Associated fauna include *Malgasaynella* and *Menuthiocrioceras* (a peculiar group of endemic heteromorphs to which *Cryptocrioceras* is herein considered to be a junior subjective synonym; Collignon 1948, 1962; Skwarko and Thieuloy 1989; Aguirre-Urreta 1990; Klinger and Kennedy 1992). Characteristic for the latest Barremian is the spreading of the Heteroceratidae from the Tethyan Realm toward the Austral Realm. Simultaneously, the Aconeceratidae, including the significant genus *Sanmartinoceras* (Fig. 9.4), most likely evolved as a separate offshoot of Desmoceratidae.

9.2.5 Aptian

In terms of ammonite paleobiogeography the Aptian is generally considered to be a cosmopolitan time due to a major transgression that begins in the early Aptian (Owen 1996). This global event was linked to the northward propagation of the Atlantic rift system, which led to the opening of numerous gateways and established new faunal connections (Rawson 1994; Hallam 1981; Bengtson & Kakabadzé 1999). The faunal dispersals are also linked to a shift toward warmer conditions that equalized climate belts and ultimately led to a global warmhouse (Föllmi 2012, with references). As outlined by Rawson (1994) and Baraboshkin (2002), this reorganization broke down the "*old Boreal/Tethyan dichotomy*" that had led to the widespread distribution of the ancyloceratid-deshayesitid assemblage during the early Aptian. As outlined by Wright et al. (1996) and Kakabadzé et al. (2004), the ancyloceratids are known by their widespread distribution in the Tethyan- (Mediterran-Caucasian Subrealm including the Caribbean area), Boreal- (Boreal-Atlantic and Boreal-Pacific subrealms) and Austral realms. However, due to homeomorphy of the body-chamber ornamentation, most ancyloceratid genera, such as *Ancyloceras*, are ill-defined taxa that are in need of revision. In our opinion, the species from the Mediterran-Caucasian and Boreal-Atlantic subrealms on which the Ancyloceratidae genera introduced by Spath (1930), Casey (1960), Vermeulen and Lazarin (2007) and Delanoy et al. (2008) are based, cannot be compared with the large tripartite heteromorphs that occur in California (Anderson 1938; Murphy 1975), Colombia (Kakabadzé and Hoedemaker 2004), South Africa (Klinger and Kennedy 1977), Japan (Shimizu 1931) and Australia (Day 1967). A similar view was expressed by Pictet et al. (2009) for *Lithancylus* taxa that are now restricted to Spain, France, England and the Russian Platform. As a consequence, endemism in Ancyloceratidae has certainly been overlooked and needs further investigation, although it is partly reflected by the introduction of such genera as *Shastoceras* from California (Anderson 1938), *Laqueoceras* from Colombia (Kakabadzé et al. 2004) and *Helicancyloceras* from South Africa (Klinger and Kennedy 1977).

Deshayesitidae are recoiled heteromorphs that evolved from heteromorphic representatives of the Heteroceratidae by a recoiling of the shell at the end of the late Barremian (Delanoy 1997; Bogdanova and Mikhailova 2004; Delanoy and Bert 2006). The family shows a wide distribution in the Tethyan and Boreal realms during the early Aptian (Bersac and Bert 2012, with references). According to the latter authors, there are no significant morphological differences between the genus *Deshayesites* and the regional genera, *Turkmeniceras*, *Prodeshayesites*, *Paradeshayesites* and *Obsoleticeras* that occur in the northern and eastern parts of the Mediterran-Caucasian Subrealm and/or on the Russian Platform and adjacent areas of the Boreal Realm. Although widely distributed, *Deshayesites* is rare or even missing in some hemipelagic and pelagic settings in the Tethys, probably due to a bathymetric and/or facies control (Landra et al. 2000; Lehmann et al. 2009). *Deshayesites* evolved anagenetically toward *Dufrenoyia*, which marks the maximum geographic extension of the Deshayesitidae in the latest early Aptian (Fig. 9.5). *Juandurhamiceras* and

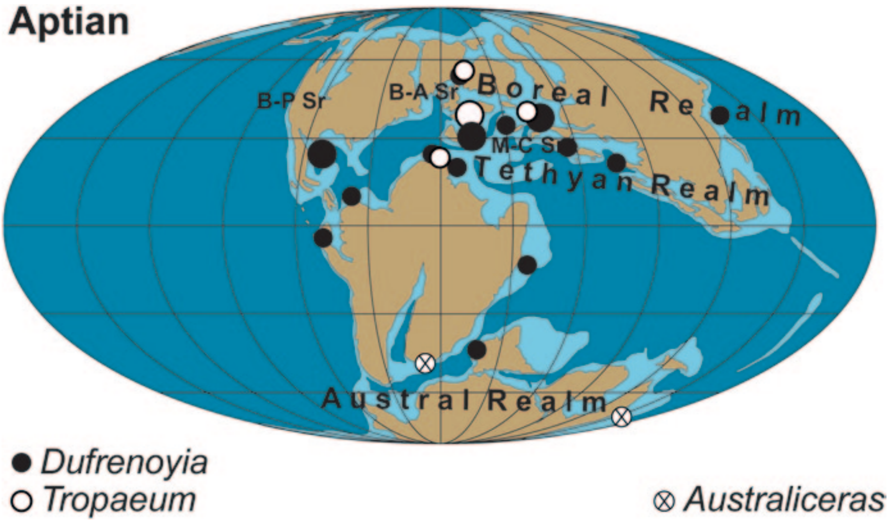

Fig. 9.5 Aspects of Aptian ammonite paleobiogeography. Map based on 120 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Burckhardtites (including *Burckhardites* reported from Turkmenistan (Bogdanova and Mikhailova 2004)) are Caribbean offshoots of *Dufrenoyia*. However, from our point of view the generic separation of these three genera also needs to be discussed carefully because of minor differences in shell shape only. The extinction of the family appears to be a sudden and almost synchronous event, marking the Lower/Upper Aptian boundary (Casey et al. 1998; Moreno-Bedmar et al. 2013).

During the continued Aptian trangression, faunas of isolated epicontinental basins show an increasing dispersal. Baraboshkin (2002), for example, recognized a Tethyan parahoplitid-douvilleiceratid and a Boreal ancyloceratid-aconeceratid assemblage around the Lower/Upper Aptian boundary on the Russian Platform. Simultaneously, large recoiled ancyloceratids occur almost worldwide, from the Austral to the Boreal Realm (Klinger and Kennedy 1977; Bengtson and Kakabadzé 1999). These forms have usually been referred to *Australiceras, Proaustraliceras* and *Tropaeum*, and are distinguished by the absence of a tuberculate stage on the inner whorls in the latter genus. Recently, McKenzie et al. (2014) argued that the two genera should be put in synonymy because the development of a tuberculate stage varies with intraspecific variability. Even if we agree that the Australian specimens attributed to *Tropaeum* in the literature (Whitehouse 1926; Day 1974) are macroconchs of *Australiceras*, comparison of the ornamental features of the early ontogeny of the European *Tropaeum* does not support the synonymy of the two genera. In our view, *Australiceras* is an endemic genus that characterizes the Austral Realm, since typical *Tropaeum* only occur on European shelves of the Mediterran-Caucasian Subrealm and the adjacent part of the Boreal Realm (Baraboshkin 2002; Fig. 9.5). *Proaustraliceras* shows a similar distribution, with no reliable records from the southern hemisphere (Kakabadzé et al. 2004). The relationships between these ancyloceratids are still obscure. Thus this group can not currently be used for defining paleobiogeographic boundaries. During the early Aptian, the Douvilleiceratidae are also a major component of the worldwide ammonite assemblage, although some genera possibly hint at a paraphyletic origin of this family. The *Procheloniceras*-*Cheloniceras*-*Epicheloniceras* lineage is characteristic of the Tethyan Realm and of the southern area of the Boreal Realm (Casey et al. 1998; Kakabadzé et al. 2004; Pictet 2012). In the late early Aptian, *Roloboceras* and *Megatyloceras,* closely-allied or possibly congeneric with *Cheloniceras*, are typically recorded during the early Aptian of the Mediterran-Caucasian Subrealm and southern area of the Boreal Realm (Casey 1961; Moreno-Bedmar et al. 2010; Ivanov and Idakieva 2013).

Dauphin (2002) documented a complex turnover in the earliest late Aptian that led to the appearance of the widespread family Parahoplitidae. This event was observed at the scale of the Tethyan Realm, from the Transcaspian to the Caribbean domains (Bogdanova and Tovbina 1995; Arnaud et al. 2002). The genus *Colombiceras* evolved from *Gargasiceras* in the late early Aptian and spread over the entire Tethyan Realm during late Aptian times, where it gave rise to the *Acanthohoplites*-*Hypacanthoplites* lineage (Bulot in Vincent et al. 2010, with references). *Colombiceras* may also be the rootstock of *Parahoplites* in the Mediterran-Caucasian Subrealm and adjacent Boreal areas, and of the closely allied genera *Sinzoviella* and *Kasanskiella* from the Caribbean. In the latest Aptian, the diversification of Acanthohoplitinae reached its peak. This is the case for *Diadochoceras* and the closely allied, if not synonymous, *Nodosohoplites,* which are considered to be an offshoot of *Acanthohoplites,* while *Neodeshayesites* is a New World derivative of *Hypacanthoplites s.l.* Other endemic genera of Acanthohoplitinae have been reported from North America (*Rhytidoplites* and *Immunitoceras*), eastern Mexico (*Penaceras*)*,* Colombia (*Riedelites*), northwestern Caucasus (*Chaschupseceras*), Japan (*Oshimaceras*) and Tunisia (*Melleguieiceras*). The phylogenetic relationships of all these genera also remain largely unclear (Bulot in Vincent et al. 2010; Latil 2011; Bulot et al. 2014).

9.2.6 Albian

Albian paleobiogeography is generally distinguished from that of the Aptian by a more pronounced provincialism, although this trend tends to diminish in the upper part of the stage (Owen 1996; Baraboshkin 2002, with references). The peak of endemism is reached in the earliest Albian, where three faunal provinces have been recognized in the Boreal Realm (Owen 1979, 1988a; Alabushev and Wiedmann 1994; Baraboshkin 2002; Jagt-Yazykova and Zonova 2012): the Boreal-Atlantic Subrealm, characterised by *Leymeriella*, *Sonneratia* and hoplitinid ammonites (the latter e.g. with *Euhoplites*, Fig. 9.6); the Arctic Subrealm, where *Arcthoplites*, *Freboldiceras* and Gastroplitininae flourished; and the Boreal-Pacific Subrealm, which was dominated by cleoniceratids (*Leconteites, Brewericeras, Grycia*). In the earliest Albian, arcthoplitid ammonites from the Arctic entered northwestern Europe and

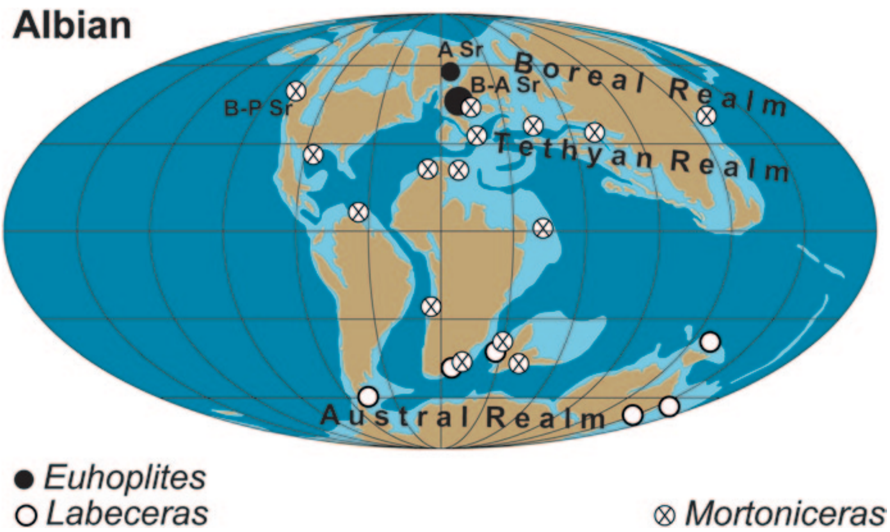

Fig. 9.6 Aspects of Albian ammonite paleobiogeography. Map based on 105 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Mangyshlak—thus these areas provide important information for the stratigraphic correlation on a global scale (Savel'ev 1973; Owen 11988a and b, 1996; Lehmann et al. 2013).

Compared to the limited area of the Boreal epicontinental shelf basins, the Tethyan Ocean had a vast expanse from northern South America and southern North America to Australia (Fluteau et al. 2007; Vrielynck 2010). In terms of ammonites, the assemblages of the Tethyan Realm mainly consist of brancoceratids (*Brancoceras*, *Prolyelliceras*, *Mirapelia*), lytoceratids (*Kossmatella*), desmoceratids (*Beudanticeras*), engonoceratids (*Parengonoceras*, *Knemiceras*, *Glotticeras*), and douvilleiceratids (*Douvilleiceras*) (Kennedy and Cobban 1976; Owen 1979, 1996; Marcinowski and Wiedmann 1990; Riccardi and Medina 2002; Robert and Bulot 2004; Bulot in Vincent et al. 2010; Latil 2011). In the earliest Albian new and distinguished families of heteromorphic ammonites (Anisoceratidae and Hamitidae) arose, spreading over most of the Tethyan Realm in the late early Albian (Monks 1999, 2002; Kennedy et al. 2000). During the early Albian the boundary between the Boreal and Tethyan realms was fairly sharp, despite scattered occurrences of *Leymeriella* on the Eurasian shelves of the northern margin of the Tethys (Kennedy et al. 2000, with references). Occasionally, in the late early and early middle Albian, *Douvilleiceras*, *Tegoceras, Lyelliceras* and *Oxytropidoceras* s.l. invaded the Boreal Realm of Europe and the northern Pacific coast of America (Owen 1971, 1988a; Amédro 1992; Amédro and Robaszynski 2005).

Different paleobiogeographic affinities between the early/middle and late Albian faunas are also recognized in the Austral Realm. However, in Australia itself these are influenced by a division into regional basins (Henderson and McKenzie 2002). In the middle Albian, fairly cosmopolitan anisoceratids and hamitids occur in the Great Artesian Basin in Australia (McNamara 1980; McKenzie 1999), but in the late Albian cosmopolitan genera occur only in the marginal areas of Australia, since, according to micro- and nannofossil data, the connection to the open ocean was restricted (Henderson and McKenzie 2002). Thus, a less diverse late Albian fauna evolved in the Great Artesian Basin, with dominant endemic heteromorph species of *Labeceras* and *Myloceras*, in contrast to the rich diversity of assemblages in Europe and elsewhere during this time interval, and only isolated records of Tethyan origin like *Goodhallites* (Henderson and Kennedy 2002). Although *Labeceras* (Fig. 9.6) and *Myloceras* characterize the ammonite province of the Austral Realm in the late Albian, endemic species developed also in the regional basins of Madagascar, southern Africa and South America (Förster 1975; Klinger 1976; Klinger and Kennedy 1989; Aguirre-Urreta and Riccardi 1988; Riccardi 1988).

During the late Albian a long-time trend toward more cosmopolitan faunas is established with the rapid rise and radiation of the Mortoniceratinae (e.g., *Mortoniceras*, Fig. 9.6) and Stolickaiellinae. However, the disappearance of the Early Cretaceous provincialism is a long-running process that did not end until the middle Cenomanian (Owen 1973; Wiedmann 1988; Ifrim et al. 2015).

Unusual insights to the paleobiogeographical affinities of Albian ammonite faunas in the Atlantic are given by a few drilling core sites of the DSDP/ODP programme (Wiedmann 1978; Wiedmann and Neugebauer 1978; Renz 1979a; Wiedmann 1988; Lehmann 2000; Owen and Mutterlose 2006). A fauna from the Biscay margin shows affinities to the Boreal realm for the early Albian, while middle to possibly late Albian ammonites indicate a Tethyan aspect (Renz 1979b). The other occurrences from the Atlantic are, as far as datable, late Albian faunas indicating strong Tethyan relations (with the Curacao debated, see Owen and Mutterlose 2006). Among these the relatively rich association from offshore Florida is remarkable, since it represents a hemipelagic or even pelagic assemblage with species with a preference for oceanic conditions and, despite the strong affinities to the Tethys, it generally reveals a cosmopolitan character (Lehmann 2000).

9.3 Conclusion and Future Perspectives

Many Early Cretaceous faunas are dominated by heteromorphic ammonites. While they play almost no role in the earliest Cretaceous, they dominate many faunal assemblages from the early late Hauterivian until the end of the Cretaceous period. However, reasons for this and most of the ecological constrains involved are still under debate, including trophic opportunities and sea-level changes (Wiedmann 1969; Nesis 1986; Cecca 1997; Keupp 2000). The global Cretaceous sea-level rise started in the Aptian, and despite an increased spreading of taxa, there is some strong provincialism in the Albian characterized by regularly coiled ammonites. This demonstrates that a complex pattern of sea-level changes and the opening and closure of seaways must be responsible for ammonite dispersal in the Early Cretaceous.

Ongoing research emphasizes that insufficient taxonomy is a factor masking paleobiogeographic affinities (Kennedy and Cobban 1976; Rawson 1993; Bengtson and Kakabadzé 1999), This is particularly true for the Berriasian, early Barremian and Aptian (present chapter). Furthermore, quantitative analyses of the spatial distribution of ammonoids—such as have been done for some other time intervals (Dera et al. 2011; Korn and Klug 2012; Korn and De Baets 2015)—are rare to absent for the Early Cretaceous Epoch. This hampers our ability to test the robustness of the paleogeographical affinities described in this chapter, and underlines the urgent need for quantitative studies earlier called for by Bengtson and Kakabadzé (1999). Therefore the interpretations presented here are thorough revisions and updates of earlier significant contributions in this field (Rawson 1981, 1993, 1994; Cecca 1998), but are likewise qualitative studies and thus still reflect a preliminary state.

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