The evolution and geography of Jurassic ammonoids

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PAGE, K.N. 2008. The evolution and geography of Jurassic ammonoids. *Proceedings of the Geologist's Association*, **119**, 35–57. Ammonites are probably the most famous marine fossil of the Jurassic System, being often abundant and with a virtually global distribution where appropriate facies are preserved. Along with their fundamental role for Jurassic stratigraphy and correlation, this frequency of occurrence and wide distribution can also provide valuable insights into Jurassic marine biogeography as well as into evolutionary and other palaeobiological processes. In the Jurassic, up to seven suborders can be recognized: Phylloceratina, Psiloceratina, Ammonitina, Lytoceratina, Haploceratina, Perisphinctina and Ancyloceratina. Each is reviewed, citing a selection of important evolutionary case histories. These suborders range through up to about 20 distinguishable biogeographical provinces and subprovinces distributed through up to seven realm-group biochores. The latter comprise a northern, high latitude Pan-Boreal Realm or Superrealm (including the Arctic, Boreal–Pacific and Boreal–Atlantic realms/subrealms) and the low latitude and southern Pan-Tethyan Realm or Superrealm (including the Mediterran–Caucasian, East Pacific, Indo-Pacific and possibly Austral realms/subrealms).

Key words: Jurassic, ammonoids, evolution, biogeography

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1. INTRODUCTION

The ammonites are perhaps the most familiar fossils of marine Jurassic rocks and are widely recognized as a 'classic' fossil type. In part, they owe this fame to their remarkable abundance globally, which in turn means they have been long associated with traditional cultural beliefs. The latter range from manifestations of former evils – as in the 'snake-stones' of the Lower Jurassic of Yorkshire – to the revered symbols of good fortune, or *Shaligramma*, from the Upper Jurassic of the Himalayas (as sold to passing pilgrims).

Scientifically, however, they are one of the most useful fossils that the System has to offer and can provide reliable global correlations and a potential stratigraphical resolution locally of little more than 100 000 years – no other fossil group or indeed any other correlative method can currently, in isolation from others, even come close to matching this in the Jurassic (Callomon, 1995; Page, 1995). This stratigraphical value is well established and need not be reviewed further here. In broader palaeontological terms, the abundance and wide distribution of ammonites can provide valuable insights into both Jurassic biogeography and evolutionary processes. The following review, therefore, provides a background to these other important facets of their study. Other aspects of ammonoid ecology and shell structure are not discussed in detail but reviews can be found in the excellent volume on ammonoid palaeobiology edited by Landman *et al.* (1996).

2. THE ORIGINS AND EVOLUTION OF JURASSIC AMMONOID SUBORDERS

Post-Triassic ammonoids (Order Ammonoidea) have been grouped conventionally into four suborders (Phylloceratina, Lytoceratina, Ammonitina and Ancyloceratina), and this classification still permeates most palaeontological textbooks. However, based on studies of sutural development, phylogeny and shell structure, Bessenova & Michailova (1983; 1991) proposed that the Suborder Ammonitina should be restricted and introduced two additional suborders, the Haploceratina and Perisphinctina. A seventh Suborder, the Psiloceratina, may also be required to maintain a phylogenetic classification of the Ammonoidea, as suggested by Page (1996), following observations on the origins of the early Ammonoidea by Guex (1987).

Other schemes are possible, but the Bessenova & Michailova (1983; 1991) framework is generally compatible with established classifications of Jurassic and Cretaceous Ammonoidea and has the added advantage of being comparable to that used for most Triassic and earlier groups of similar rank, thereby reducing the misleading impression of a greater suborder-level diversity in the Triassic (cf. Page, 1996).

There still remain many open questions about ammonoid taxonomy and evolution which will be answered only through detailed stratigraphically controlled studies at the level at which evolution actually took place – the species. Genera, families and all higher taxa are often no more than convenient groupings of

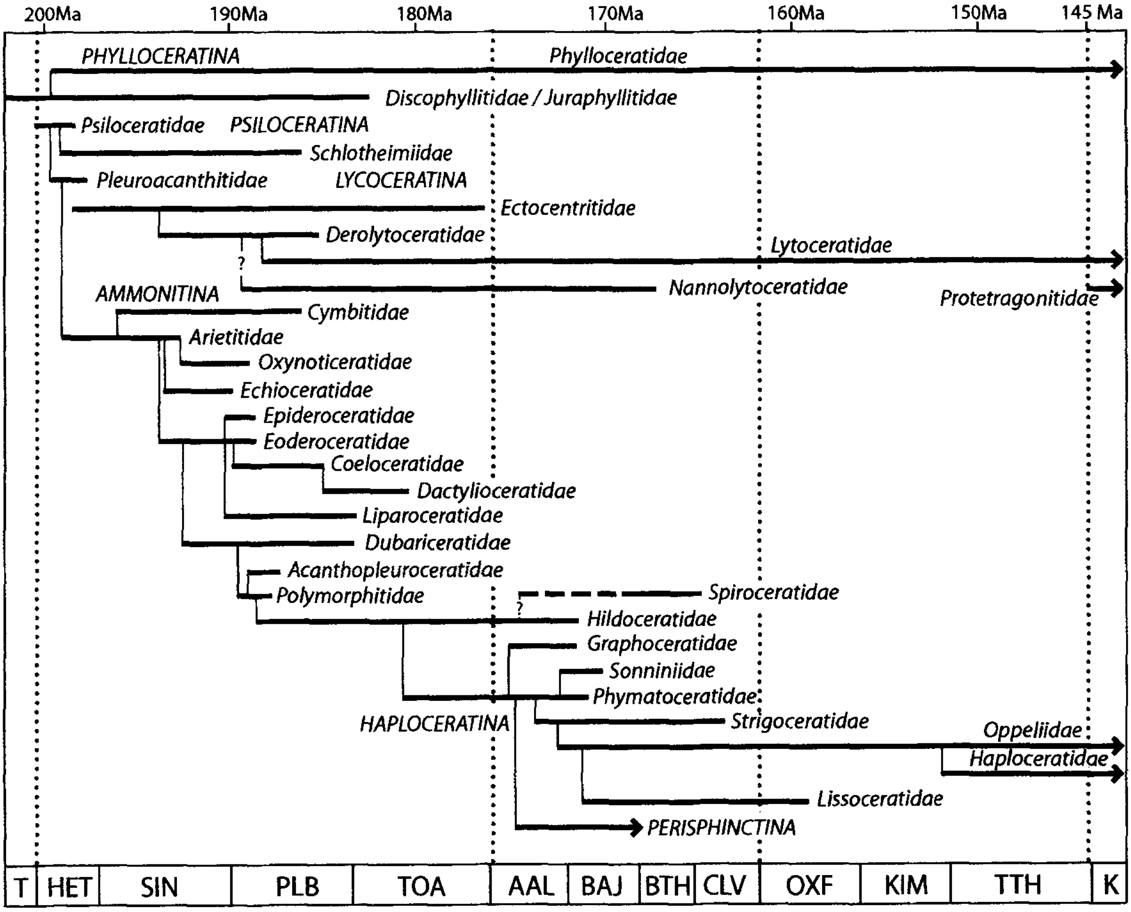


Fig. 1. Ranges of Jurassic ammonite families of the suborders Phylloceratina, Psiloceratina, Lytoceratina, Ammonitina and Haploceratina. Updated from Page (1993); some evolutionary links conjectural. Dates based on International Commission on Stratigraphy standard; T, Triassic; HET, Hettangian; SIN, Sinemurian; PLB, Pliensbachian; TOA, Toarcian; AAL, Aalenian; BAJ, Bajocian; BTH, Bathonian; CLV, Callovian; OXF, Oxfordian; KIM, Kimmeridgian; TTH, Tithonian; K, Cretaceous. Superfamily assignment as follows: Phylloceratidae to Juraphyllitidae (Phylloceratoidea), Psiloceratidae to Schltheimiidae (Psiloceratoidea), Pleuroacanthitidae to Nannolytoceratidae (Lytoceratoidea), Protetragonitidae only (Tetragonitoidea), Cymbitidae only (Cymbitoidea), Arietitidae to Echioceratidae (Arietitoidea), Epideroceratidae to Polymorphitidae (Eoderoceratoidea), Spiroceratidae only (Spiroceratoidea), Hildoceratidae to Phymatoceratidae (Hildoceratoidea), Strigoceratidae to Lissoceratidae (Haploceratoidea).

broadly similar shell forms and have varying degrees of phylogenetic reality. However, even at the basic species level, the often marked sexual dimorphism and frequently wide morphological variability of the shells of many ammonite species means that some authors continue to classify different shell shapes as different species and place them within different genera or even subfamilies. This practice not only creates spuriously enhanced ammonoid diversities, it also confuses taxonomic frameworks and evolutionary pathways. Kennedy & Cobban (1976) still provide a useful review of these problems; other key discussions or demonstrations of ammonoid dimorphism, intraspecific variation and its taxonomic consequences include Callomon (1963, 1981, 1985) and Westermann (1966).

The standard word endings used in the taxonomic hierarchy are -ina (Suborder), -oidea (Superfamily), -idae (Family) and -inae (Subfamily). The stratigraphic ranges of the suborders and their component families are shown in Figures 1 and 2.

Suborder Phylloceratina

The Phylloceratina are virtually the only ammonoid group to have survived the end-Triassic extinctions and give rise, just below the Triassic–Jurassic boundary, to all later Mesozoic ammonoids via the Family Psiloceratidae. Morphologically, the Suborder is exceptionally conservative and characterized by sutures with ovoid tips to finely divided lobes (i.e.

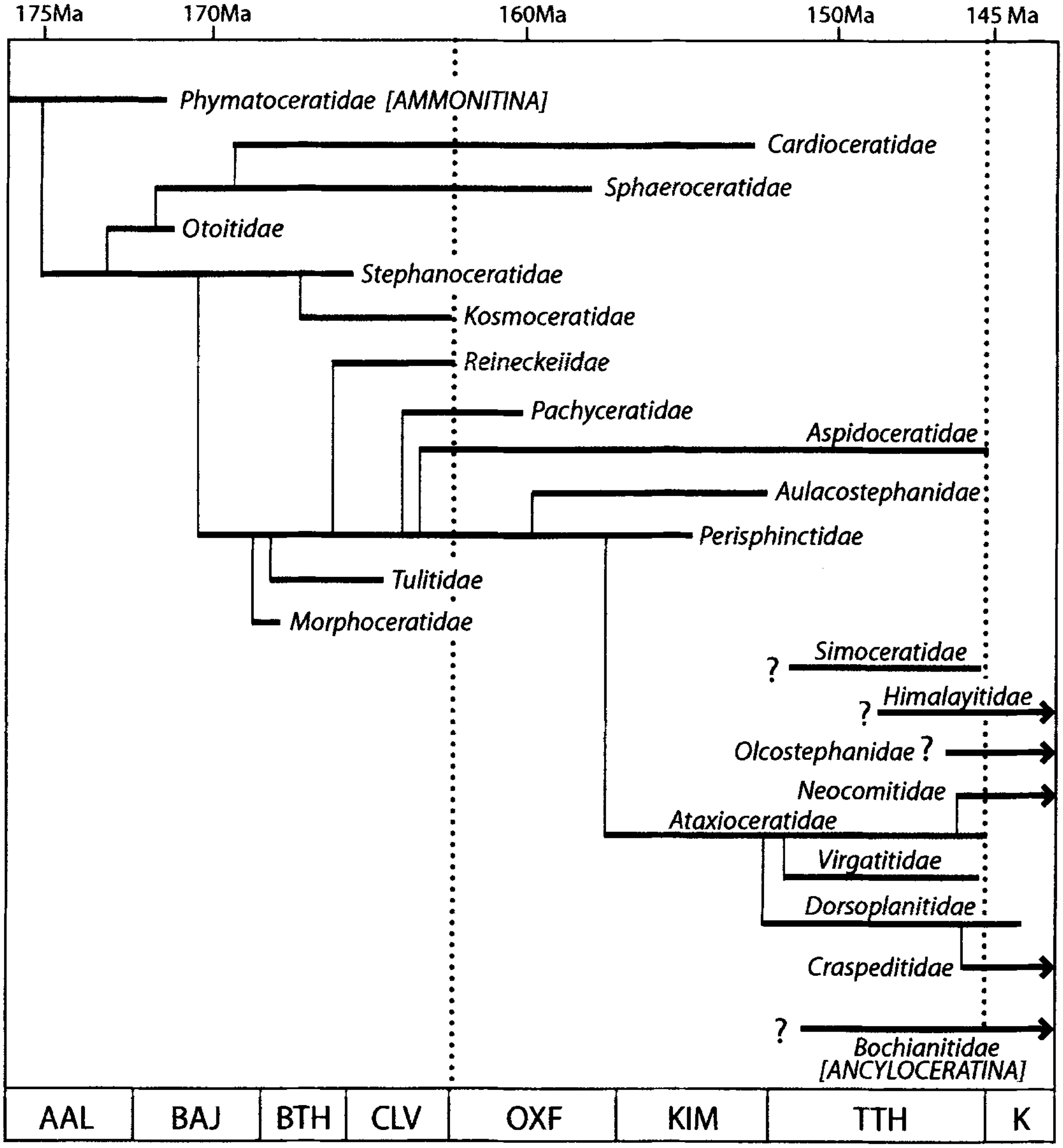


Fig. 2. Ranges of Jurassic ammonite families of the suborders Perisphinctina and Ancyloceratina. See Figure 1 for details. Stephanoceratidae to Cardioceratidae (Superfamily Stephanoceratoidea), Reineckeiidae to Craspeditidae (Superfamily Perisphinctoidea).

a 'phylloid' style). In the Triassic, their shells tend to be relatively evolute, compressed and smooth, and this style persisted into the Early Jurassic where some developed ornament such as plications (Family Juraphyllitidae). A second group, the Family Phylloceratidae, evolved in the early Hettangian, with involute, round-ventered shell morphologies, frequently with shell constrictions or flares and with little more than fine growth lines as ornament. Sexual dimorphism is often cryptic as many faunas are dominated by juveniles or nuclei with few adult shells usually available. However, within the Juraphyllitidae, clear dimorphism is often observed with small and larger forms. Both show simple, sinuous apertures which follow growth lines and, as a result, have little more than short ventral rostra-like projections. Slight ventral projection of rib-like plications near the mature aperture does, however, appear to be a characteristic of some microconchs.

The Phylloceratina range from the Early Triassic (Nammalian) to latest Cretaceous (latest Maastrichtian) and are widely distributed globally.

Most genera, however, are associated primarily with low latitude Tethyan regions, where the group was often very abundant and – with the similarly distributed Lytoceratina – often comprises more than 50% of the recorded ammonoid fauna and locally over 80% (Donovan, 1967; Géczy, 1976). It is likely that this distribution reflects an adaptation to deeper-marine environments, as Phylloceratina are often most abundant in deeper-water areas subject to oceanic influences – even at relatively high latitudes – and uncommon or absent in neighbouring shelf sea areas. Further evidence for such a habitat comes from their shells, which could survive crushing to greater depths than any other ammonoids (Hewitt & Westermann, 1987). However, the Juraphyllitidae include exceptions to this rule, such as *Tragophylloceras*, which became locally abundant in the Pliensbachian of NW Europe (Meister, 1993). The development of a sub-oxyconic shell and plications in some species, combined with conspicuous dimorphism, makes the genus morphologically and ecologically distinct from most other Phylloceratina.

Suborders Psiloceratina and Ammonitina

The first Jurassic ammonite – the small, typically smooth and planispiral genus *Psiloceras* – appeared in the latest Triassic and was a direct descendant of Late Triassic Phylloceratina such as *Rhacophyllites*. This latter genus is a member of the Family Discophyllitidae, which is only questionably distinct from the Juraphyllitidae, and probably the only other ammonoid survivor of the end-Triassic extinctions. Traditional views of the origins of later Ammonitina involve the development of a keel on the evolute, ribbed and slightly younger psiloceratid *Caloceras* (e.g. Arkell *et al.*, 1957) – hence producing the first members of the Superfamily Arietitoidea. A parallel lineage retained a simple venter and gave rise to the relatively involute psiloceratoidean Family Schlotheimiidae, the earliest members of which are distinctly evolute and *Caloceras*-like.

However, sutural development and other features led Guex (1987) to propose that *Psiloceras* not only gave rise to all later Psiloceratoidea (including the Schlotheimiidae) but also, separately, to the Arietitoidea, via the genus *Pleuroacanthites*, a member of the Superfamily Lytoceratoidea and Suborder Lytoceratina. As observed by Page (1996), in a phylogenetic classification of the Ammonoidea, such a scheme would imply that either the Lytoceratoidea belong with the Suborder Ammonitina (*sensu* Bessenova & Michailova, 1983, 1991), or that the Superfamily Psiloceratoidea should be assigned to a suborder of their own – the Psiloceratina. The latter scheme is assumed here. In both Ammonitina and Psiloceratina, sutures are ammonitic but vary in complexity; the primary suture of both suborders is five-lobed, although possibly grading into a four-lobed form (Bessenova & Michailova, 1991). However, in species of Psiloceratina, including the Schlotheimiidae, sutural lobes frequently have 'phylloid' tips.

As *Psiloceras* and its close relatives evolved through the earliest Jurassic, they demonstrate a trend common amongst many later Jurassic ammonite groups. Tethyan species, such as *P. calliphyllum* (Neumayr), often have complex sutures, whereas NW European *P. planorbis* (J. Sowerby) and *P. psilonotum* (Quenstedt) have simpler sutures (Schlatter, 1994). Earliest Hettangian *Psiloceras* and its descendant *Caloceras* both show well-developed dimorphism simply expressed through two size classes of complete shell. Dimorphism is more classically expressed amongst their descendants, the strongly ribbed Family Schlotheimiidae, which had appeared by the mid-Hettangian; wholly ribbed microconchs and larger macroconchs which typically lose their ribbing on middle and outer whorls are characteristic – although apertures always remain simple. A general trend from evolute, round-whorled forms (*Waehneroceras*) in the mid-Hettangian to compressed involute forms in the Late Sinemurian (e.g. *Angulaticeras*) is apparent. A possible late representative of the Schlotheimiidae (and hence of the Psiloceratina) in the Early Pliensbachian is *Phricoderoceras* which shows a return to thicker whorled forms. However, the same style of dimorphism remains, with strongly ornamented microconchs and macroconchs with high and weakly ribbed outer whorls.

The restricted Suborder Ammonitina includes a much wider range of shell morphologies, ranging from evolute serpenticones to inflated sphaerocones and compressed oxycones. Ornament is also much more varied than in the Psiloceratina and includes clearly differentiated primary and secondary ribs, nodes and spines, and ventral grooves and keels, in numerous styles and combinations. Shell dimorphism is also characteristic although, in some of the earlier Superfamily Arietitoidea, it is manifested mainly as differences in size and only occasionally are significant differences in the adult morphology of each dimorph recognizable (mainly the weakening of ribs on the body-chamber of macroconchs). Apertures remain simple in both dimorphs, although short, ventral, rostra-like projections of the keel are typical. However, in some groups such as the later Subfamily Arnioceratinae, including *Arnioceras* itself, small smooth but keeled microconchs with very slightly flared, simple apertures accompany larger macroconchs with identical inner whorls, but sharply ribbed and keeled middle and outer whorls. In the Subfamily Asteroceratinae, microconchs are again ribbed to the end, but may show some weakening of ventrolateral grooves towards the mature, simple aperture. Macroconchs have a tendency to become almost smooth on their body-chambers and with more compressed and higher whorls.

Several distinct evolutionary trends are recognizable in the Arietitoidea, one of the most distinctive being the gradual progression from evolute-ribbed Arietitidae, such as *Arietites* and *Pararnioceras*, with well-developed bisulcate–tricarinate venters in the Early Sinemurian, to more involute *Caenisites* and *Asteroceras*, with weakened lateral sulcae and keels in the mid-Sinemurian, and then the rapid development via intermediate *Eparietites* of compressed, oxycone forms, such as *Oxynoticeras* and *Gleviceras*, in the Late Sinemurian. A similar, but earlier development of oxyconic forms takes place in the Early to mid-Sinemurian, with the progression from *Coroniceras* to *Paracoroniceras* and ultimately *Agassiceras*. However, the earliest representatives of the Arietoidea, the Alsatitinae of the mid to late Hettangian, are always very evolute, with only simple ribbing and a keeled venter, typically without sulcae.

In some later families of the Superfamily Hildoceratoidea, dimorphism is more classically developed, with macroconchs having simple apertures and microconchs paired lateral lappets. The latter features are perhaps first seen in microconchs of Early Toarcian *Hildoceras*, as figured by Howarth (1992), although these remain little more than an expression of biconvex growth lines. However, in the Subfamily Leioceratinae and all later groups (e.g. Family Graphoceratidae), lappets have become a discrete modification of the aperture on mature microconchs.

A number of well-developed evolutionary progressions have been recognized within the Hildoceratoidea which are often of great stratigraphical value. One of the most important is that of *Hildoceras* (Family Hildoceratidae) in the Early Toarcian, from its origins within tricarinate–bisulcate and biconvex ribbed *Hildaites* through a range of species in which a smooth band develops on the inside of the whorl followed by a lateral groove (Gabilly, 1976). Each stage in this progression can be used to distinguish a sequence of high resolution, sub-subchronozone correlative units known as horizons (Elmi *et al.*, 1997). There is also some evidence of dwarfism, as suggested by differences in septal spacing, indicating different growth rates within isolated populations in several small Tethyan basins (Mignot *et al.*, 1993).

Evolute to involute progressions are also recognizable, for instance in Early Toarcian Harpoceratinae (Family Hildoceratidae) and Hammatoceratinae (Family Phymatoceratitidae). In the Pliensbachian, the evolution of sub-oxyconic, keeled *Amaltheus* from evolute, round-ventered *Aegoceras–Oistoceras* (Family Liparoceratidae) is well documented, as is the 'reversion' to more evolute morphologies in later *Pleuroceras* (Dommergues, 1987; Meister, 1988). However, in the Graphoceratidae of the Aalenian and Early Bajocian, although overall trends are not identified so readily, the ultimate expression of the group is oxyconic *Hyperlioceras*. The family is well developed throughout Europe and well-preserved faunas, such as those from the Aalenian and Bajocian 'Inferior Oolite' of southern England, have meant that it has experienced more than its fair share of taxonomic 'splitting' – most notably by S. S. Buckman (1887–1907; 1909–30). Nevertheless, this artificially inflated diversity underlies a genuinely high degree of stratigraphical differentiation which facilitated the establishment of detailed sequence of correlatable, high-resolution biohorizons by Callomon & Chandler (1990).

The development of the spinose Family Eoderoceratidae in the late Early Sinemurian, although probably from the arietitid Subfamily Agassiceratinae, is more cryptic, as is their connection with Pliensbachian Polymorphitidae and hence the Liparoceratidae. Dommergues & Meister (1999) attempted to resolve the problematic relationships within these and other Eoderoceratoidea through cladistic analysis and produced a revised framework of included families. However, considerations such as relationships with the important Toarcian group, Family Dactylioceratidae, remained unresolved, and it seems likely that the Eoderoceratoidea are polyphyletic. Indeed, the strong similarity of some of their earlier members, the Eoderoceratidae, to Lytoceratina has often been quoted as an example of 'iterative' evolution from a conservative stock (e.g. Arkell *in* Arkell *et al.*, 1957).

The Suborder Ammonitina also includes a small and short-lived group of Mid-Jurassic heteromorph ammonites, the Superfamily Spiroceratoidea, which evolved in the later Bajocian and persisted until at least the early Mid-Callovian (Dietl, 1978). The origins of the group lie within the hildoceratoidean genus *Tmetoceras* and morphologies range from loose spirals to forms with U-bends linked by straight shafts.

Psiloceratina and Ammonitina have a world-wide distribution from their first appearance as *Psiloceras* in the earliest Hettangian – undoubtedly representing a sudden expansion to fill an ecospace created by the demise of most other ammonoid groups in the Late Triassic. Very early on, however, some provincial differentiation seems to be recognizable initially at species, and subsequently at generic or even family, level. This endemism defines most of the biochores of the Early to early Mid-Jurassic, excepting where Phyllo- and Lytoceratina dominate, and diversities were typically highest at lower latitudes – as with most marine organisms. Few other trends are discernible, although low latitude, deeper-water Tethyan groups frequently have more complex sutures than their epicontinental contemporaries, as noted above. In addition, a few groups with apparent origins in trans-equatorial areas, such as the Subfamily Bouleiceratinae (Family Hildoceratidae), show simplified sutures (often termed 'pseudoceratitic') which, as throughout the Mesozoic, seem to be typical of ammonite groups that originated in regions for which there is evidence of environmental restriction, perhaps abnormal salinities. Indeed, Triassic *Ceratites* itself and its allies appear to have adapted to such environments (Uhrlichs & Mundlos, 1980). Ceratitic sutures, therefore, appear to have more to do with ecology than phylogeny – despite still being presented as an evolutionary link between the goniatitic and ammonitic-sutured ammonoids in many standard textbooks.

Suborder Lytoceratina

In common with the Phylloceratina, the Lytoceratina show great evolutionary conservatism throughout their range from the earliest Jurassic to the latest Cretaceous. Shell morphologies are usually evolute, rarely ribbed and typically possess complex, even moss-like, non-phylloid sutures. The presence of regular internal constrictions, sometimes underlying external flares of the shell, is a common and characteristic feature. The first Lytoceratina appeared in the earliest Jurassic and have no obvious Triassic ancestors. However, as suggested by Guex (1982), their origin may lie within the earliest Jurassic Psiloceratina. Dimorphism is often cryptic and, as with the Phylloceratina, often masked by the incompleteness of available material. However, in the Late Toarcian, a pairing of small, strongly constricted *Alocotlytoceras* and giant '*Megalytoceras*', the latter with essentially smooth outer whorls, seems likely.

The Lytoceratina have very similar distribution patterns to those of the Phylloceratina, the two groups commonly occurring in association in deeper-water facies of the Jurassic and Cretaceous. There is, however, some suggestion that latitudinal controls may have been more important for the Lytoceratina, as high-latitude records seem to be less common than for the Phylloceratina, and the former are typically only abundant in low latitude Tethyan faunas. Occasionally, however, the Lytoceratina stray from their preferred home and, at several levels in the Pliensbachian and Toarcian of NW Europe, they are locally common. Such forms tend to have simpler sutures than their ocean-going cousins, and the latter also have stronger septa and siphuncles – an important adaptation to deeper-water environments (Hewitt & Westermann, 1987; Westermann, 1996).

Suborder Haploceratina

The Haploceratina are a long-ranging suborder with origins in the early Mid-Jurassic Superfamily Hildoceratoidea. These origins are somewhat cryptic, but may lie within the Hammatoceratinae of the Family Phymatoceratidae (Donovan *et al.*, 1981). Shell morphologies are predominantly compressed, often tending towards platyconic or oxyconic shapes with relatively weak ornament; smooth mature forms, even microconchs, are frequent. Keels are often present and, more rarely, ventral grooves. Dimorphism is well developed and similar to that of some late Hildoceratoidea, with simple-apertured macroconchs, and microconchs with well-developed, even spatulate, lappets (e.g. Callomon, 1981). Sutures are ammonitic and often complex in macroconchs, the primary form being five-lobed (Bessenova & Michailova, 1991). However, in some groups, such as the Clydoniceratinae of the Family Oppeliidae, the sutures are simplified, a possible response to environmental stresses such as higher-than-normal salinities for its early, low latitude members (e.g. *Micromphalites*), and lower-than-normal salinities for its later NW European descendents (*Clydoniceras*; Page, 2001). The simple, weakly or unornamented shells mean that the stratigraphical value of the Haploceratina is often limited and confusion between species easily arises; a notable example is the renaming of the 'Aspidoides Zone' of the Upper Bathonian as the 'Orbis Zone', necessitated when the type horizon of the original index, *Oxycerites aspidoides* (Oppel), was subsequently confirmed to be Upper Bajocian (Dietl, 1982). Some groups of Haploceratina are stratigraphically more useful; these include certain oppeliid subfamilies, such as the Hecticoceratinae (Bathonian to Early Oxfordian) and the Taramelliceratinae (Callovian to Kimmeridgian); both, not surprisingly, have a stronger and more distinctive ornament style with differentiated ribs and sometimes nodes.

The Haploceratina range from the Mid-Jurassic (Aalenian) to the Late Cretaceous (Santonian). They are characteristic of low latitude Tethyan areas and tend to be rare or absent in northern, high latitude Boreal regions. However, in 'intermediate' areas, including the Submediterranean and NW European provinces in Europe, they can be locally common at some stratigraphical levels.

Suborder Perisphinctina

The Perisphinctina are typical of most Mid-Jurassic to Cretaceous ammonoid faunas. The group is morphologically very diverse, with a wide range of ribbing styles, including secondary or even tertiary subdivision, bullae, nodes and spines. Keels are generally absent in Jurassic groups, although they re-evolve in some families, such as Callovian–Kimmeridgian Cardioceratidae. Dimorphism is typically very well developed, with lappeted microconchs and smooth-apertured macroconchs, and has often led to dimorphs being assigned to different genera, even subfamilies (e.g. Arkell *in* Arkell *et al.*, 1957). Sutures are characteristically ammonitic and may be complex in some groups, the primary form being five-lobed (Bessenova & Michailova, 1991).

The origins of the Suborder lie in the Toarcian–Aalenian Subfamily Hammatoceratinae of the Family Phymatoceratidae, and probably from the genus *Erycites* (Donovan *et al.*, 1981) through loss of a keel and the development of a broadly rounded venter. The earliest Stephanoceratoidea vary from very thin and evolute Stephanoceratidae to involute and inflated Otoitidae. Primary ribbing is typically modified as lateral tubercles and linked to secondary ribs which cross the venter essentially uninterrupted.

By the later Early Bajocian, the globular Sphaeroceratidae had appeared, a family which would later become important as endemic East Pacific and Indo-Pacific Eurycephalitinae (Bajocian–Bathonian) and extending to Mediterran–Caucasian areas as the Macrocephalitinae (Bathonian–Mid-Callovian). In Indo-Pacific areas, the Family persisted until the earliest Kimmeridgian as the Mayaitinae. Unlike most other Stephanoceratoidea, microconchs of the Sphaeroceratidae lost their lappets early on and both dimorphs show simple apertures, but often with some degree of apertural constrictions on slightly eccentric outer whorls. Ribbing is unmodified by tuberculation but often multibranched, passing uninterrupted over a rounded venter, but frequently fading on the body-chamber of macroconchs. Assemblages often show an extreme range of variation from coarsely ribbed and relatively inflated, to compressed and finely ribbed forms, and the effects of a marked provincialism can make correct identification difficult. For the Late Bathonian to Mid-Callovian, published lists of recorded species can consequently be, at best, misleading; for example in Jeannet (1954), 22 Indian, south-east Asian and European Macrocephalitinae species names were mixed up to describe what is little more than a single variable biological species from a single bed in the Swiss Jura (Page, 1988).

The evolution of the Family Cardioceratidae from its origins in the Boreal Early Bathonian *Cranocephalites*, through the Cadoceratinae of the Late Bathonian–Mid-Callovian to the Cardioceratinae of the Late Callovian–Kimmeridgian, is one of the classic stories of Jurassic ammonite evolution (Callomon, 1995). The early forms have rounded whorls similar to their sphaeroceratid ancestors, but macroconchs soon develop depressed cadicone morphologies, with microconchs becoming relatively compressed. In both dimorphs, the venter becomes increasingly arched and ultimately develops a keel, as in typical *Cardioceras*. Ribbing in later forms is clearly differentiated into primaries and secondaries but, by the Mid-Oxfordian, it also begins to become increasingly projected, modified or interrupted, sometimes with tubercles and bullae. Apertures are simple in macroconchs, although often showing a terminal constriction on a smooth body-chamber. Like its ancestors, microconchs are not lappeted and are ribbed to the end of their body-chambers which develop short ventral rostra. Intra-specific variation is often extensive, with inflated, even depressed, coarse-ribbed forms alongside compressed finely ribbed morphologies (as illustrated by Callomon, 1985).

In the later Bathonian and Callovian, the Family Kosmoceratidae evolved in Boreal areas from a stephanoceratid ancestor, such as *Cadomites*. Early forms are relatively evolute and round-whorled (*Kepplerites*), but develop a tabulate venter on compressed and involute whorls (*Kosmoceras*). Ribbing is clearly differentiated into secondaries and primaries with lateral nodes and then spines developing. The latter are relatively large in some later Callovian microconchs, including the appropriately named morphogenus '*Spinikosmoceras*'. The abundance of Kosmoceratidae in the soft Oxford Clay of the brickpits of eastern England led to one of the most famous micro-evolutionary studies of any fossil invertebrate group (Brinkmann, 1929). Detailed collecting and measurement allowed the recognition of gradual changes in features such as ribbing density. These results have often been quoted (e.g. Callomon, 1963; Raup & Crick, 1981, 1982), although often perpetuating one of the basic misconceptions of the original study – that the dimorphs belong to different genera or subgenera and that variants of both dimorphs belong to different species (e.g. Lehmann, 1981). As Brinkmann retained few of the specimens he measured, his results cannot be revised adequately or updated. However, Raup & Crick (1982) noted a key lesson for studies of ammonite evolution – that although overall morphological trends may exist, especially when viewed with hindsight, detailed evolutionary 'patterns' are essentially irregular and different characters develop at different rates and in different 'directions'. In other words, there is no pre-ordained evolutionary 'goal' as is often implied in studies focusing on the paedomorphic or peramorphic processes which have been claimed to be recorded in the development of ammonoid shells.

In the Bajocian, a group of evolute stephanoceratids gave rise to the first Perisphinctoidea, the globally most important ammonites of the Late Jurassic. Members of this superfamily are typically evolute with well-developed lappets on ribbed microconchs; larger macroconchs have simple apertures and a tendency for the ribbing to weaken on outer whorls. Ribbing is generally well-differentiated into primaries and secondaries but, in some Kimmeridgian and Tithonian groups, tertiary branching is also developed. Periodic whorl constrictions are also typical in some groups. Bajocian Perisphinctoidea belong to the subfamilies Leptosphinctinae and Parkinsoniinae although, by the Bathonian and into the Callovian, the Pseudoperisphinctinae dominate (all these belong to the Family Perisphinctidae). These earlier groups often show a slight ventral weakening or interruption of ribbing but, in the Mid-Callovian, the development of the genus *Alligaticeras* (as illustrated by Cox, 1988) without such interruption, marks the beginning of the true Perisphinctinae and, hence, most later Jurassic and indeed Cretaceous ammonite groups. Perisphinctoidea consequently dominate most Tethyan ammonite faunas for the remainder of the Jurassic, and with the demise of the Stephanoceratoidea in the Kimmeridgian, also take over Boreal areas.

A recurring problem of perisphinctoidean taxonomy is the high degree of homeomorphism, resulting in a great similarity between different taxa from widely different stratigraphical levels and palaeogeographical regions. Following an attempt to establish a primarily phylogenetic classification of the group, Callomon (*in* Donovan *et al.*, 1981) reported '... a family tree of almost innumerable trunks and branches of all lengths and thicknesses'. Enay & Cariou (1997) expanded the theme and noted that the Perisphinctoidea were

> … a large, dendroid evolving group, the phyletic relationships of whose components are poorly understood in spite of the many models proposed. Perisphinctids show a large variety of ribbing, coiling and whorl shape and the current systematics express the morphological similarities rather than the phyletic relationships: so the same generic names are used for homeomorphs, [and] sometimes heterochronic taxa, without any true relationships.

Only now is this taxonomic mélange being unravelled and a considerable amount of recent work in continental Europe and elsewhere is finally beginning to extract genuine palaeobiological and stratigraphical meaning from the taxonomic 'dustbins' of the past.

The main, conservative, perisphinctoidean stocks (families Perisphinctidae, Ataxioceratidae, Virgatitidae and Dorsoplanitidae) gave rise to a number of other groups in which morphologies became increasingly specialized. These include the spinose families Aspidoceratidae and Reineckeiidae, the inflated and relatively involute Tulitidae and Pachyceratidae, and the flat-sided, tabulate-ventered Neocomitidae. The Tulitidae appear in the Early Bathonian and, although initially evolute and perisphinctoid, develop a trend towards more involute, cadicone or sphaerocone forms. Although body-chambers may be markedly eccentric, and body-chambers and apertures constricted, short lappets demonstrate their perisphinctoidean affinities. The Family Pachyceratidae of the Late Callovian and Oxfordian also often has relatively inflated morphologies, although its earliest members, in the Mid-Callovian, are more perisphinctoid and more clearly derivable from contemporary Pseudoperisphinctinae (Callomon *in* Donovan *et al.*, 1981). Lappets are secondarily lost in microconchs of later Pachyceratidae.

The first major spinose group, the Family Reineckeiidae, appeared in the Bathonian as perisphinctoid forms showing affinities to Pseudoperisphinctinae or earlier subfamilies – including a characteristic ventral interruption of the ribbing. Macroconchs typically have one or more rows of strong tubercles often replacing primary ribs and linked to short secondary ribs; the lappeted microconchs, however, remain perisphinctoid throughout, with a characteristic reineckeiid bunching of secondary ribs against a short primary and with a ventral smooth band. The Aspidoceratidae also first appear in the early Mid-Callovian and probably had a similar origin. They include the Subfamily Peltoceratinae with macroconchs developing heavy nodes or spines, although retaining typical wiry, branching perisphinctoid ribbing on their inner whorls. Microconchs have similar ribbing throughout but this may become distinctly rursiradiate towards the end of the lappeted body-chamber. In the Aspidoceratinae, however, the ribbed stage is lost in typical macroconchs, which rapidly develop a stout, often quadrate section and two rows of spines without linking ribs. Microconchs are more evolute with relatively blunt ribbing. Nuclei of both dimorphs have weak irregular ribbing with 'parabolic nodes' – a distinct and periodic modification of the ribbing. This feature links them to a different Pseudoperisphinctinae group – specifically *Grossouvria* and its relatives which have similar ribbing modifications on their nuclei – suggesting that the Aspidoceratidae, as conventionally recognized, are polyphyletic. In the Tithonian, the Perisphintoidea diversified further, giving rise to a range of more specialized, compressed and often spinose families including the Himalayitidae, Olcostephanitidae, Neocomitidae and Polyptychitidae – the last three of which are more typical of the Cretaceous than the Jurassic.

The Perisphinctina range from the Mid-Jurassic (Aalenian) to the end of the Late Cretaceous (Maastrichtian) and show some of the most dramatic geographically controlled distributions of any ammonoid group. In part, this reflects the dynamics of Mid and Late Jurassic palaeogeography, but also a remarkable ability within the group to adapt to a range of different environments. Differentiation was at species, genus, subfamily, or even family level and the northern high latitude/low latitude, or Boreal/Tethyan Superrealm separation, was usually the most pronounced. Recent reviews, however, suggest that a Southern Hemisphere, mid- to high-latitude Austral Realm, or at least Subrealm, might also be recognizable by the end of the Jurassic (Enay & Cariou, 1997, 1999).

Suborder Ancyloceratina

The last of the ammonoid suborders to evolve, the Ancyloceratina, include all the well-known heteromorph ammonoids of the Cretaceous and their immediate ancestors in the latest Jurassic. The earliest Ancyloceratina appeared in the Early Tithonian and belong to the loosely coiled genus *Protancyloceras* (Family Bochianitidae) and are completely unrelated to earlier Jurassic heteromorphs. The origins of *Protancyloceras* are, however, obscure but are presumed to lie in contemporary Perisphinctina, perhaps in certain very evolute late Idoceratinae, such as Kimmeridgian *Mesosimoceras* (which has simple ribbing and occasional ventrolateral tubercles, not unlike those of *Protancyloceras*). Jurassic Ancyloceratina are rare and known only from low latitude Tethyan areas. The Suborder ranges from Tithonian to latest Cretaceous (Maastrichtian).

3. THE GEOGRAPHY OF JURASSIC AMMONOIDS

Terminology

A common problem in the recognition of bioprovincialism in any fossil group is a general lack of systematic information on the relative abundance of different taxa in different regions. As a result, faunal lists give as much or even enhanced significance to rare taxa as they do to the common and more characteristic, and the frequent misidentification of local faunas adds further confusion. Combined with a lack of consistency in the methodology and terminology used by different authors, it can be very difficult to trace true biogeographical relationships and differences reliably.

Faced with this scenario, the informal discussion group *'Friends of Palaeobiogeography'* was established in 1996, leading to the publication of a series of guidelines for the recognition of marine biogeographical units – or *biochores* – in the Mesozoic (Westermann, 2000a, b). Such biochores are typically defined by the overall level of endemism observed (i.e. geographical restriction of taxa) within specific geographical and chronological limits. The guidelines confirmed a hierarchy of ranks or tiers which could be applied to recognized units, depending on the scale or persistence of each unit, ranging from Superrealm (having major differences, for instance at family level), through Realm, Subrealm, Province to Subprovince, where differences may be at the level of relative abundance of different taxa, and endemism little more than at species level. Within this hierarchy, only Realm and Subrealm are considered to be 'obligatory' catagories.

In the Jurassic and Cretaceous, Westermann (2000a, b) considered seven marine realm-level biochores to be of general value, although not all persisted throughout this time interval or indeed co-existed at any one time. These biogeographical units could be distinguished at either full realm or subrealm level and were grouped into two superrealms or realms – the Pan-Boreal and Pan-Tethyan. These are equivalent to the 'traditional' Boreal and Tethyan realms of most previous authors. Crucially, these units were established on the basis of distributions of a range of marine macrofossils, including bivalves, not just ammonoids.

The evolution of ammonoid provincialism through the Jurassic

The same basic pattern of continental distribution (with the single supercontinent of Pangaea) persisted from the Triassic into the Early Jurassic and ammonoid distributions are, not surprisingly, very similar (Page, 1996; Fig. 4). Throughout the Jurassic, a high northern latitude Pan-Boreal Superrealm or Realm (including the Arctic, Boreal–Pacific and Boreal–Atlantic realms/subrealms) is recognizable, with a much broader Pan-Tethyan Superrealm or Realm (including the Mediterran–Caucasian, East Pacific, Indo-Pacific and Austral realms/subrealms) to the south, including high southern latitudes. The use of the terms Superrealm vs. Realm and Realm vs. Subrealm depends on the scale of the faunal differences, which vary through time.

Boreal faunas were often of low diversity, reflecting environmental stresses at high latitudes. Tethyan faunas occupied both the northern (i.e. Laurasian) and southern (i.e. Gondwanan) shores of the Tethys Ocean, from western Europe eastward to southeast Asia and then around Australasia and the Jurassic South Pole to the East Pacific seaboard and the margins of the proto-Pacific Ocean (i.e. Panthalassa; Fig. 4). Tethyan faunas can, therefore, include both low latitude, high diversity Northern and Southern Hemisphere faunas, and low diversity, high latitude Southern Hemisphere faunas. Nevertheless, strong faunal similarities frequently exist between these areas at generic and sometimes species level. During phases of increased endemism, however, especially in the Mid- and latest Jurassic, significant generic differences are noticable and endemism may include examples at subfamily or even family level. At such times, several co-existing realms or subrealms are recognizable.

Although in the earliest Jurassic, East Pacific areas, such as the western USA and Canada, had some distinctive faunal elements, a substantial number of genera are shared with Mediterran–Caucasian areas, suggesting that some faunal interchange was possible (Figs 4 and 5). Whether this involved polar traverse, an oceanic crossing or some sort of short cut between the Pacific and European areas via a proto-'Hispanic Corridor' (cf. Westermann, 1993) is not yet certain. These similarities consequently place all lower latitude Northern Hemisphere and all Southern Hemisphere – including high latitude – in a single Mediterran–Caucasian Realm.

By the Late Pliensbachian, Boreal areas already showed sufficient differentiation that three realms/subrealms are recognizable (Arctic, Boreal–Atlantic and Boreal–Pacific; Westermann, 2000b; Figs 3 and 5) and this basic framework persisted throughout most of the rest of the Jurassic (at least when marine connections were open between the Arctic and Europe). At a similar time, East Pacific faunas first begin to show a significant level of endemism and an East Pacific Realm or Subrealm becomes recognizable (Westermann, 1993, 2000a, b). The latter typically occupies the entire Panthalassa Ocean seaboard from the Antarctic to the boundary with the Pan-Boreal Superrealm/Realm in the Northern Hemisphere. The Mediterran–Caucasian Realm mirrors this pattern on the east side of the supercontinent, from south to north, and includes both the southern and northern shores of Tethys (Figs 4 and 6).

In the Mid-Jurassic, faunal exchange around Tethys became more difficult and a Southern Hemisphere Indo-Pacific Realm or Subrealm becomes recognizable at mid to high latitudes on the south side of Tethys, at least by the Bathonian (Westermann, 2000a, b). By the end of the Jurassic, Indo-Pacific Realm faunas had spread to higher latitudes along the southern seaboard of Panthalassa, perhaps signalling the first appearance of a distinctive, Southern Hemisphere, high latitude Austral Realm or Subrealm, as discussed by Enay & Cariou (1997, 1999; Figs 4 and 7).

Within Europe, the brief establishment of uninterrupted north–south, Tethys Ocean–Boreal Sea

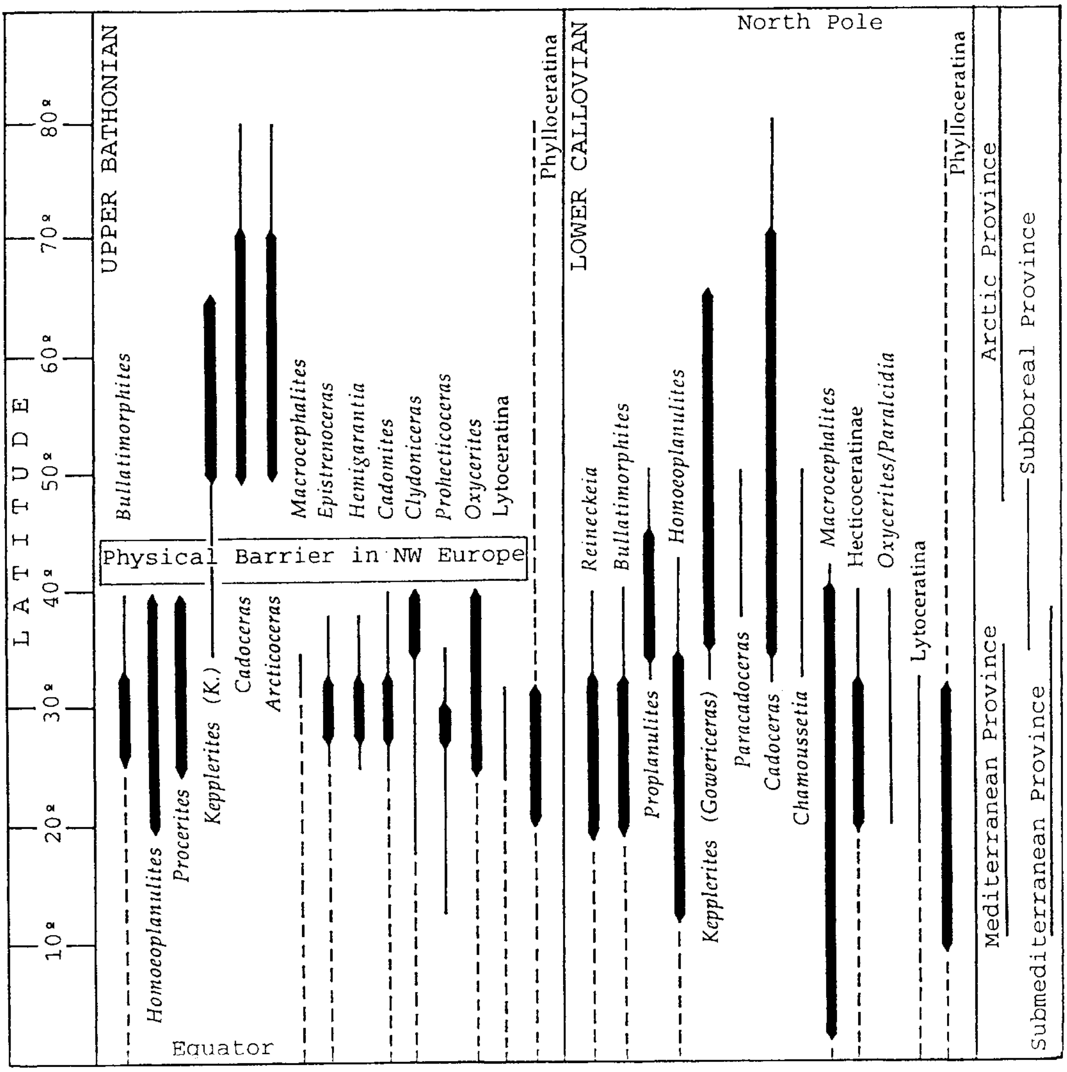


Fig. 3. The establishment of latitudinal control on ammonites faunas in Europe following the breakdown of physical barriers to migration at the Bathonian–Callovian boundary. Thick lines indicate common occurrence, thin lines rare records and dashed lines link to Southern Hemisphere records (i.e. genera may still occur at these Jurassic latitudes but were not quoted specifically in sources used).

connections in the later Early Jurassic and again from the late Mid to near the end of the Jurassic, provided new possibilities for faunal interchange. Latitudinal, rather than physical, controls on faunal character and diversity dominate and a series of essentially east–west provincial belts developed. Typically, these show a passage from very low diversity and high latitude Arctic (or 'Boreal') assemblages, through transitional Subboreal and Submediterranean to low latitude Mediterranean assemblages (Figs 3 and 6). Significantly, however, Submediterranean assemblages may be some of the most diverse, as Mediterranean assemblages tend to reflect deeper-water environments, not suited to all taxa. However, each province in this progression had a distinctive fauna, not only in terms of the relative abundance of different taxa, but also in the presence or absence of particular species, genera and subfamilies. Towards the end of the Jurassic, the establishment once more of physical barriers separating Boreal and Tethyan areas in Europe meant that interchange was no longer possible, thereby creating major problems for global correlation at the Jurassic–Cretaceous boundary (Figs 4, 7 and 8; see Cope, 2008).

A similar transition from low latitude diverse faunas to higher latitude restricted faunas is also detectable south of the Jurassic equator towards the Antarctic, although the recognition of discrete latitudinal bioprovinces is often less straightforward. Nevertheless,

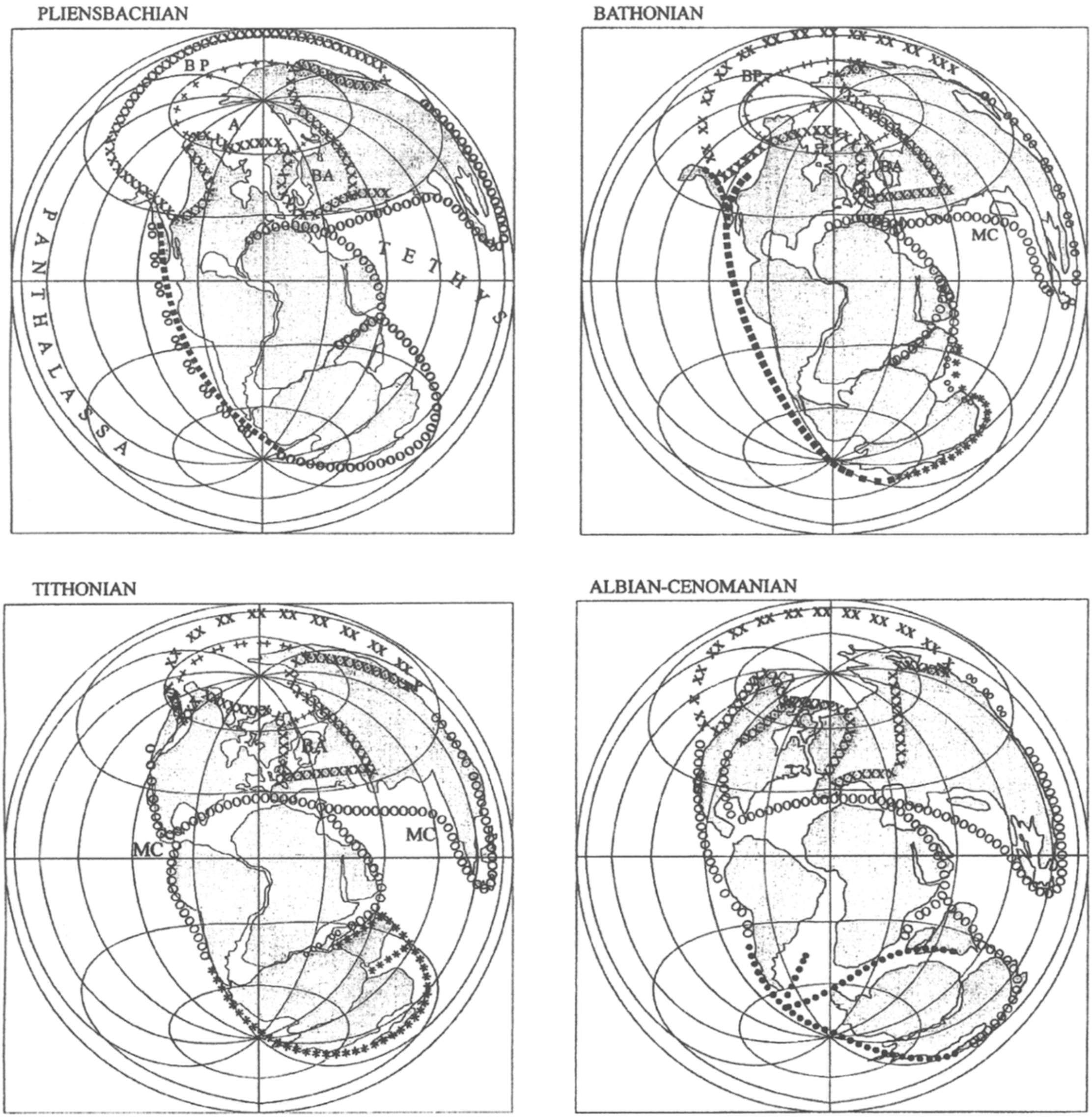
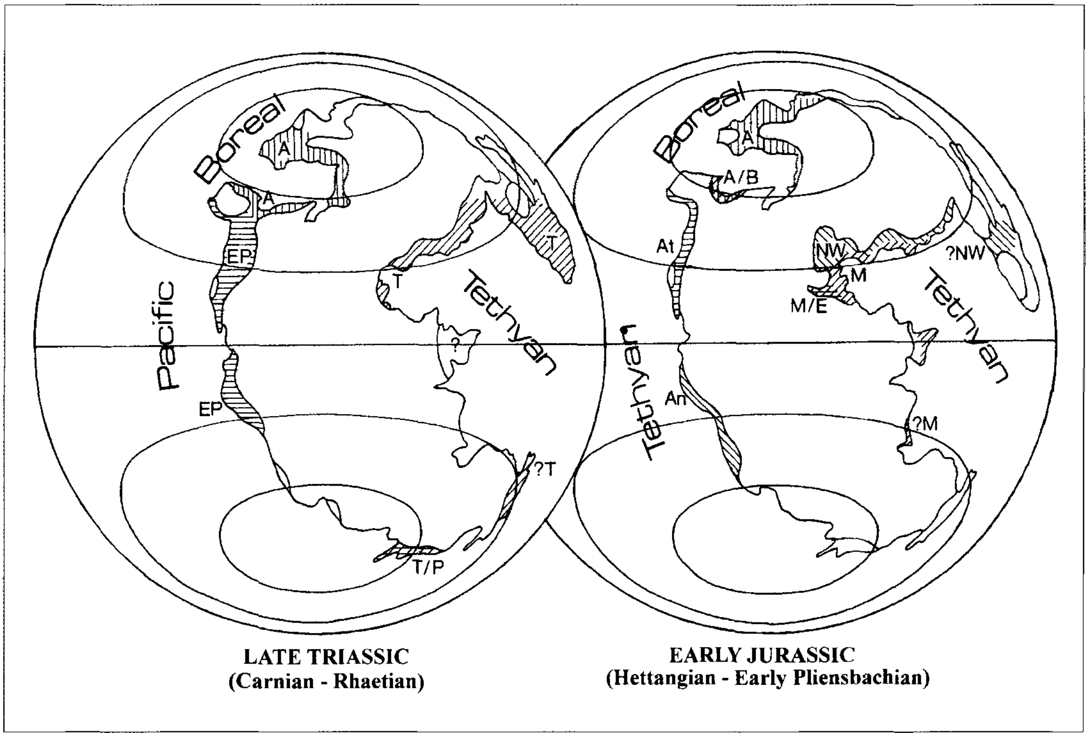


Fig. 4. Realm-group marine biochores from the Early Jurassic to the earliest Late Cretaceous. *Pan-Boreal Superrealm/ Realm* (limits indicated by xxxx): A, Arctic Realm/Subrealm; BP, Boreal–Pacific Realm/Subrealm; BA, Boreal–Atlantic Realm/Subrealm (limits of each Realm/Subrealm indicated by ++++). *Pan-Tethyan Superrealm/Realm*: MC, Mediterran–Caucasian Realm/Subrealm (limits indicated by oooo); East-Pacific Realm/Subrealm (limits indicated by ■■■■), Indo-Pacific Realm/Subrealm (limits indicated by ****), Austral Realm/Subrealm (limits indicated by ●●●●). Reprinted from *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 163, G.E.G. Westermann. Marine faunal realms of the Mesozoic: review and revision under the new guidelines for biogeographic classification and nomenclature. pp. 40–68, ©2000, with permission from Elsevier.

within the Andean Province, a low latitude, high diversity Antofagusta Subprovince and a high latitude, lower diversity, Neuquén Subprovince are recognizable by the later Mid-Jurassic (Fig. 6). With the establishment of the Indo-Pacific and ultimately the Austral realms, a more or less symmetrical pole-to-pole pattern of ammonoid diversity changes is finally established. These basic underlying distribution patterns are occasionally modified at different levels in the Jurassic by the development of further distinct regions or provinces characterized by one or more endemic or very restricted genera or species. Physical barriers to migration, such as land, restricted marine or deep-marine environments (and associated currents), would



LATE TRIASSIC
(Carnian - Rhaetian)

EARLY JURASSIC
(Hettangian - Early Pliensbachian)

Fig. 5. Jurassic ammonoid provinces through time: Late Triassic to Early Jurassic (Carnian–Early Pliensbachian). A, Arctic; An, Andean; At, Athabascan; B, Bering; E, Ethiopian; EP, East Pacific Realm/Subrealm; M, Mediterranean; NW, NW European; T, Tethyan 'Region'; T/P, 'mixed' Pacific/Tethyan Realm. Continental projection modified from Smith & Briden (1977). A modified version appears in Page (2005).

have been significant factors, but there also seems to be some indication that purely ecological preferences or adaptations were also at work in some species.

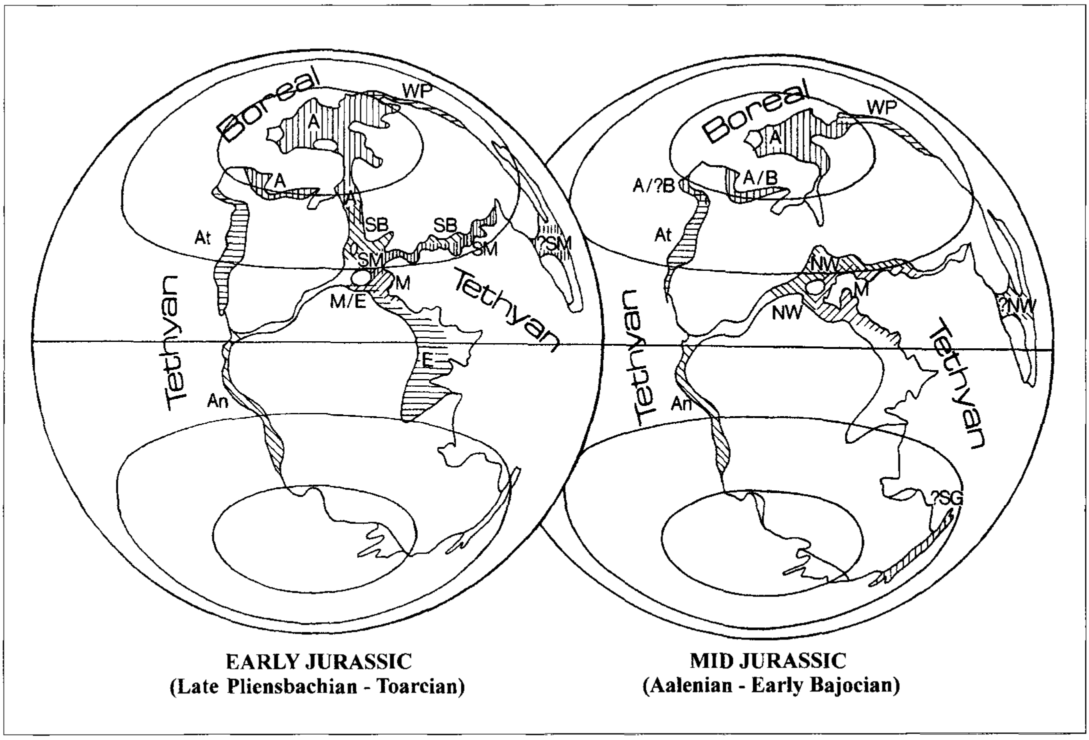
The development of migration pathways along seaways, as discussed by Westermann (1993), periodically permitted interchange between different provinces and realms, most notably between the western Tethys and East Pacific, via the Hispanic Corridor, and between Boreal and west Tethyan areas within Europe, via the Viking Corridor. As a consequence of the operation of these intermittent barriers, the appearance or disappearance of, in particular, genera can appear diachronous when traced from one faunal province to another (Westermann, 1993). A lack of appreciation of such controls on ammonite distributions can lead to significant correlation errors, as perpetrated by Jenkyns *et al.* (2002) when attempting to demonstrate the global synchrony of the famous Early Toarcian anoxic event on the basis of the first record of the genus *Hildoceras* (Family Hildoceratidae) in Mediterranean and Subboreal areas. The stratigraphical information presented, however, indicates two different 'events' or even a diachronous phase of anoxia.

About 20 distinct faunal provinces or subprovinces are generally recognized during the Jurassic. Most of these existed for relatively short intervals and certainly at no time were all co-existent. Nevertheless, the Mediterranean Province is recognizable throughout the Jurassic, and the Arctic Province is clearly distinguishable from the Late Pliensbachian onwards. Due to changing marine connections, some of these provinces may change their affinities, for instance from Tethyan to Boreal and back again, although as their areal extent often remained similar, renaming following each change is not considered necessary (cf. Westermann, 2000a, b).

Pan-Tethyan Superrealm

Mediterran–Caucasian Realm/Subrealm

Mediterranean (or West Tethyan) Province [M] (southern Spain, Italy, Austria, Hungary, Bulgaria, North Africa, etc.). The Mediterranean Province is characteristic of relatively deep-water facies open to the influence of the Tethys Ocean and distinguished by the typical dominance of Phyllo- and Lytoceratina, which often make up over 50% of the recorded assemblage (Donovan, 1967; Géczy, 1976). Associated ammonites are generally similar to those of neighbouring NW European or Submediterranean provinces although, in the Late Jurassic, a number of perisphinctoidean genera appear to be most characteristic of



EARLY JURASSIC
(Late Pliensbachian - Toarcian)

MID JURASSIC
(Aalenian - Early Bajocian)

Fig. 6. Jurassic ammonoid provinces through time: Late Pliensbachian to Early Bajocian. See Figure 5 for details; additionally, SB, Subboreal; SG, Sula–New Guinean; SM, Submediterranean; WP, West Pacific.

Mediterranean areas, and much rarer to the north. Mediterranean Province faunas are the most consistently recognizable throughout the Jurassic.

The Family Psiloceratidae, and then Schlotheimiidae, dominate the non-Phyllo- and Lytoceratina in the Hettangian and include a number of essentially endemic species. From the mid-Hettangian, Arietitidae become increasingly important, including both Alsatitinae and early Arietitinae and with some endemic genera and species (including *Pseudaetomoceras*). The Arietitidae subsequently dominate in the Sinemurian and are replaced largely by Polymorphitidae in the Early Pliensbachian, with Hildoceratidae dominating in the Late Pliensbachian and Toarcian. Although faunas are broadly similar to their NW European counterparts, some endemic species are present and also a few genera, such as *Tmaegoceras* (Arietitidae) in the Sinemurian, and *Praesphaeroceras*, *Diaphorites* and *Pimelites* (all Coeloceratidae) in the Pliensbachian. Dactylioceratidae were only common in the earliest Toarcian. Phymatoceratidae become typical in the Late Toarcian and remain common into the Aalenian in association with typical Leiceratinae (Family Hildoceratidae) and Graphoceratidae.

Bajocian faunas of the Mediterranean Province are characteristically diverse, with the place of the Phymatoceratidae taken by their descendants, the Sonniniidae. The Superfamily Haploceratoidea becomes locally abundant, especially Oppeliidae and Lissoceratidae, as do Stephanoceratoidea (including the families Otoitidae, Stephanoceratidae and Sphaeroceratidae) and later the first Perisphinctidae (including the subfamilies Leptosphictinae and Parkinsoniinae). The Perisphinctidae diversified further in the latest Bajocian and through the Bathonian to produce varied Pseudoperisphinctinae and new families, such as the Morphoceratidae and Tulitidae. Stephanoceratidae persisted, including the Cadomitinae; Oppeliinae and Hecticoceratinae (both Family Oppeliidae) are often abundant. The Macrocephalitinae (Family Sphaeroceratidae) are typical of Early Callovian assemblages, as are late Tulitidae. Pseudoperisphinctinae are generally abundant, with new perisphinctoidean families including the Reineckeiidae, Aspidoceratidae and Pachyceratidae. Oppeliidae, including Hecticoceratinae, are also often abundant. By the Oxfordian, varied Perisphinctinae (Family Perisphinctidae) often dominate the non-Phyllo- and Lytoceratina and, as before, are generally very similar to adjacent Submediterranean areas; the Aspidoceratidae, Pachyceratidae and Oppeliidae are also very similar. A few genera, however, such as *Passendorferia* (Family Perisphinctidae) appear to be most typical of Mediterranean areas and much rarer in adjacent Submediterranean areas. In the Kimmeridgian, a similar pattern persisted, with

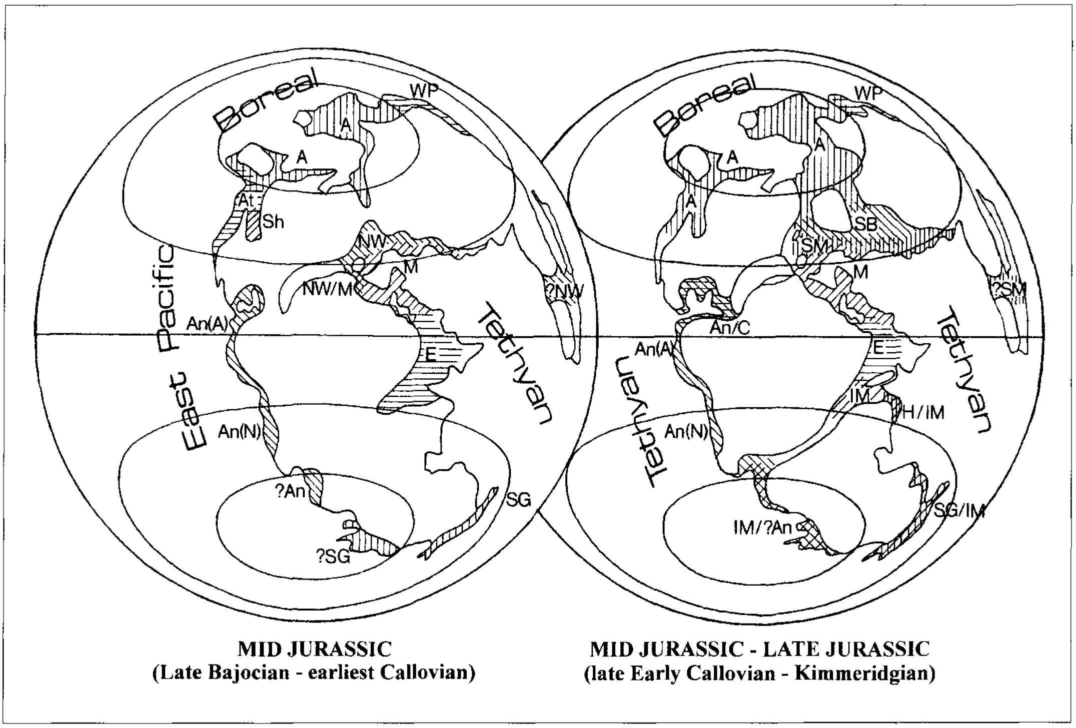


Fig. 7. Jurassic ammonoid provinces through time: Late Bajocian to Kimmeridgian. See Figures 5 and 6 for details; additionally, An(A), Antofagusta; An(N), Neuquen; C, Cuban; IM, Indo-Malgach; Sh, Shoshonean; WP, West Pacific.

widespread Taramelliceratinae (Oppeliidae) and Aspidoceratidae now in association with Ataxioceratidae. Perisphinctoidean family-level diversity increases further through the Tithonian with the arrival of the families Simoceratidae, Himalayitidae and Olcostephanidae; Haploceratidae also became important.

Representative literature on the province includes: Cariou *et al.* (1985), Cecca (1999), Cecca *et al.* (2002), Dommergues & Meister (1991), Donovan (1967), Elmi *et al.* (1997), Geczy (1976) and Page (2003).

NW European Province, including Lusitanian Subprovince [NW] (Britain, Ireland, France, Spain, Portugal, Germany, Switzerland, Caucasus, etc.). From the Hettangian to the Early Pliensbachian and again from the Late Toarcian to the Bathonian when no direct Boreal connection existed, ammonite faunas across northern and western Europe showed great similarity. Unlike the Mediterranean Province, Phyllo- and Lytoceratina were generally rare or absent, although certain species are locally common at a few levels in the Pliensbachian and Toarcian. However, the non-Phyllo- and Lytoceratina of NW European areas are generally very similar to those of a contemporary Mediterranean Province. The diversity of earlier NW European Province faunas was often low, reflecting the relatively small number of 'available' genera so soon after the Late Triassic extinctions.

In the Hettangian, typical pandemic Psiloceratidae and Schlothemiidae genera include restricted or even endemic species, although Arietitidae do not become dominant until the Early Sinemurian. In the mid-Sinemurian, some Eoderoceratidae appear to be largely restricted to the Province but other genera and species are again very similar to those in Mediterranean areas. However, limited endemism at specific level within polymorphitid faunas in Portugal may justify the separation of a Lusitanian Subprovince in the Early Pliensbachian (Dommergues & Mouterde, 1987). In the Late Pliensbachian and Early Toarcian, the NW European Province is replaced by a Submediterranean to Subboreal transition (see below) but, when north–south connections once more broke down in the Late Toarcian, widespread Grammoceratinae (Hildoceratidae) – as found in Mediterranean areas – are typical, together with less common Phymatoceratidae. Non-Phyllo- and Lytoceratina of the NW European Province remain very similar to those of Mediterranean areas until the earliest Callovian, when direct Tethyan–Boreal connections in Europe were once more established. However, a marked decrease in ammonoid diversity northwards, from central France to northern England, as observed through the Bathonian, is due to ecological factors such as lowered salinities and not to any latitudinal control or Boreal affinities (*contra* Mangold & Rioult, 1997) as no connection then existed (Page, 2001; Fig. 3).

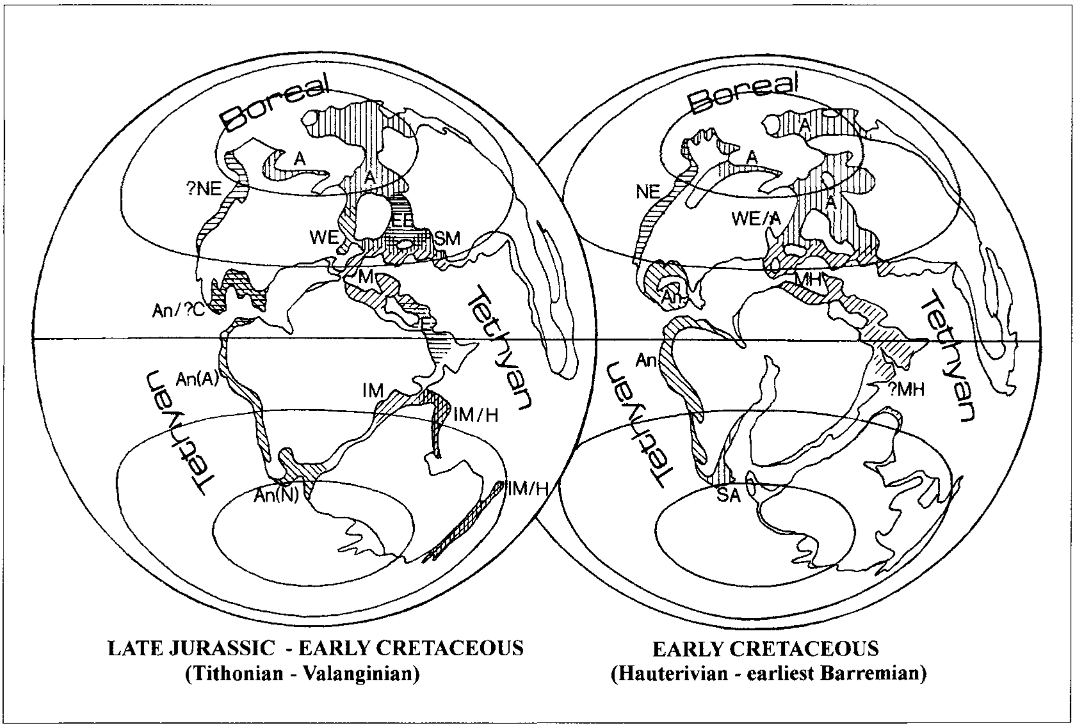


Fig. 8. Jurassic ammonoid provinces through time: Tithonian to Early Barremian. See Figures 5–7 for details; additionally, EE, East European; H, Himalayan; MH, Mediterranean–Himalayan; NE, Northeast Pacific; SA, South Atlantic (not Jurassic); WE, West European.

Representative literature on the province includes: Callomon & Chandler (1990), Contini *et al.* (1997), Dommergues (1987), Dommergues & Mouterde (1987), Dommergues *et al.* (1997), Elmi *et al.* (1997), Mangold & Rioult (1997), Mouterde & Corna (1997), Page (2001, 2003), Page & Meléndez (2000) and Rioult *et al.* (1997).

Submediterranean Province [SM] (northern Spain, southern and central France, southern Germany, Switzerland, etc.). Submediterranean faunas are first recognizable in Europe from the Late Pliensbachian to the Early Toarcian when connections between Boreal areas and Tethys were first established. Their development parallels that of a separate Subboreal Province within Europe, the two provinces together occupying essentially the same area as the former NW European Province. The Province is again recognizable from the mid-Early Callovian to the end of the Jurassic and, as before, occupied the epicontinental seas bordering the northern margins of Tethys. As in the NW European Province, Phyllo- and Lytoceratina are generally uncommon, although ammonoid diversities may be relatively high. Late Pliensbachian and Early Toarcian faunas are dominated by a variety of Hildoceratidae, largely indistinguishable from those of Mediterranean areas, with Dactylioceratidae typically being common only in the earliest Toarcian. From the Callovian onwards, a similar pattern was re-established and Perisphinctoidea are abundant, with Haploceratoidea at many levels. Endemism is limited, however, although some restricted species of *Macrocephalites* (Family Sphaeroceratidae) are present in the Early Callovian and in the Oxfordian, endemic species of Perisphinctinae (including of *Martelliceras*) appear to be present, with the genus *Larcheria* being virtually restricted to the Province.

Representative literature includes: Cariou *et al.* (1985), Dommergues *et al.* (1997), Elmi *et al.* (1997), Geyssant (1997), Hantzpergue *et al.* (1997), Page (2003) and Thierry *et al.* (1997).

Ethiopian (or 'Arabo-Malgach') Province [E] (North Africa, Ethiopia, Saudi Arabia, Israel, Turkey, Madagascar, western India, etc.). Compared to contemporary Submediterranean assemblages, faunas of the trans-palaeoequatorial Ethiopian Province were generally of relatively low diversity but consistently include endemic elements. This phenomenon probably reflects an environmental control, such as restricted or even hypersaline environments; apparent responses in the ammonite fauna include simplified or pseudoceratitic sutures. Ethiopian Province-type faunas are perhaps first recognizable in the Sinemurian, when endemic Asteroceratinae (Family Arietitidae) appear in North Africa (*Ptycharietites*, *Oxynoticeratoides* etc).

In the Toarcian, restricted or endemic faunas are characterized by Bouleiceratinae (Family Hildoceratidae) and Phymatoceratidae, including endemic *Nejdia*. A similar pattern continues into the Mid-Jurassic, with endemic genera including *Ermoceras* (Family Stephanoceratidae) in the Late Bajocian, *Thambites* and *Dhrumites* (Oppeliidae) in the Bathonian, and *Pachyerymnoceras* (Pachyceratidae) in the Callovian. A few pandemic associated Mediterran–Caucasian genera are also recorded and occasional Phyllo- and Lytoceratina. In the Tithonian, however, faunas appear to be richer and include a range of essentially endemic Ataxioceratidae (including *Phanerostephanus*, *Nannostephanus*, *Pseudinvoluticeras*) and Oppeliidae (*Oxylenticeras* and *Uhligites*). Haploceratidae, Olcostephanidae and Neocomitidae are also recorded.

Representative literature on the province includes: Cariou *et al.* (1985), Cecca (1999), Dommergues *et al.* (1986), Enay & Mangold (1984) and Zeiss (1984).

West Pacific Province [WP] (Japan, far eastern former USSR, SE Asia (part)). Although apparently retaining a generic base similar to that of contemporaneous Submediterranean or NW European province faunas, endemic species and, perhaps, genera developed in the area at various times through the Jurassic. In the Late Pliensbachian and Early Toarcian, these include species of *Protogrammoceras* (Family Hildoceratidae) and in the Aalenian, the endemic genus *Hosoureites* (Graphoceratidae). Records of Indo-Pacific taxa in the Bathonian, however, probably represent faunas of displaced or exotic terrains.

Representative literature on the Province includes: Hillebrandt *et al.* (1992a, b), Sato (1992) and Westermann (1981).

Indo-Pacific Realm/Subrealm (pre-Tithonian), Austral Realm/Subrealm (Tithonian only)

Indo-Malgach Province [IM] (Kenya, Madagascar, northwestern India, Sula Isles). Faunas of this Southern Hemisphere province were often relatively diverse, recalling Submediterranean areas at least to subfamily level. Generic differences often exist, however, and many Indo-Malgach species were different from Submediterranean forms. The former province is, in many ways, the southern equivalent of the latter, occupying the southern margin of Tethys at latitudes south of the Jurassic equator similar to those at which the Submediterranean Province was to the north. Latitudinal control of generic distribution is clearly evident, with related species apparently surviving in equivalent positions north and south of the Jurassic equator. Some limited interchange maintained similarities, at generic level at least, although this was sufficiently rare to allow distinct species to develop (Page, 1996). Phyllo- and Lytoceratina are occasionally present but do not seem to be common.

Although some endemic species of pandemic genera appear to be present in the Hettangian and Sinemurian, the Indo-Malgach Province is clearly recognizable first in the Callovian, with a range of endemic species and genera including Sphaeroceratidae (*Macrocephalites*, *Subkossmatia*, etc.) and Perisphinctidae (*Indosphinctes*, *Choffatia*, *Kinkeliniceras*, etc.) in association with pandemic Mediterran–Caucasian genera of Oppeliidae, Reineckeiidae and Aspidoceratidae. This general composition persisted into Oxfordian times, with the place of the Macrocephalitinae taken by the endemic Mayatinae (Family Sphaeroceratidae). As in the Submediterranean Province, Perisphinctinae (Family Perisphinctidae), such as *Martelliceras* and *Orthosphinctes*, are characteristic but do seem to be represented by different species. Aspidoceratidae and the oppeliid Subfamily Taramelliceratinae are also present as in the Northern Hemisphere. Throughout the Kimmeridgian, however, although there is a parallel appearance of Ataxioceratidae in Indo-Malgach areas, differentiation is also commonly at the level of genus, faunas including Southern Hemisphere (i.e. Indo-Pacific) *Torquatisphinctes* and endemic *Pachysphinctes*. Taramelliceratinae also persist. By the Tithonian, a wide range of restricted Indo-Pacific/Austral genera and endemic species appear to be present, although often obscured by taxonomic confusion with European faunas (Enay & Cariou, 1997, 1999). Ataxioceratidae (including endemic or restricted *Pachysphinctes*, *Virgatosphinctes*, *Aulacosphinctoides* etc.) are abundant, and Himalayitidae, Neocomitidae (including endemic *Blanfordiceras*), Aspidoceratidae and endemic Streblitinae (Family Oppeliidae; *Uhligites*, etc.) are also typical.

Representative literature on the province includes: Cecca (1999), Hillebrandt *et al.* (1992a, b), Krishna (1983), Sato (1992) and Sukampto & Westermann (1992).

Sula–New Guinea Province [SN] (Eastern Indonesia, Papua New Guinea). Although showing some similarities to Indo-Malgach faunas, a number of endemic taxa at generic and specific level are present during the Bajocian, Bathonian and Callovian. Phylloceratina appear to occur relatively frequently, probably due to the proximity of open ocean, rather than any significant faunal link with true Mediterranean Province areas. In the Bathonian, endemic Sphaeroceratidae (*Praetulites*, *Satoceras*, species of *Macrocephalites*) are characteristic, with Indo-Pacific *Xenocephalites*. Typical pandemic genera of Stephanoceratidae, Pseudoperisphinctinae and Oppeliidae are also present, but apparently mainly as different species from their European counterparts. Callovian species are also different from European species, but appear to have close affinities to Indo-Malgach forms. The Sula–New Guinea Province was comparable in latitude to the Subboreal Province of NW Europe and seems to show a similar faunal diversity – and certainly fewer genera than the lower latitude Indo-Malgach Province. Occasional East Pacific Realm taxa, such as *Xenocephalites*

(Family Sphaeroceratidae), indicate that some connection existed and that faunal exchange was possible around the Antarctic.

Representative literature on the province includes: Hillebrandt *et al.* (1992a, b), Sukampto & Westermann (1992) and Westermann (1993).

Himalayan Province [H] (Himalayas, Pakistan, Tibet, etc.). At certain times in the Jurassic, in particular during the Callovian and Tithonian, endemism at both generic and species level occurred in this region, suggesting a provincial status. The affinities of these faunas are always Tethyan in style, often with close links to Indo-Malgach assemblages. Some Phyllo- and Lytoceratina are recorded. In the Callovian, the characteristic elements are again Sphaeroceratidae, including endemic *Grayiceras*. However, associated Pachyceratidae, Perisphinctidae and Oppeliidae appear to show Indo-Malgach affinities. Tithonian assemblages are also close to Indo-Malgach, with similar Ataxioceratidae, Himalayitidae, Neocomitidae (including *Blanfordiceras*), Aspidoceratidae and Oppeliidae (e.g. *Uhligites*). Representative literature on the province includes: Cariou *et al.* (1994), Enay & Cariou (1997, 1999), Krishna (1983) and Krishna *et al.* (1982).

Mediterran–Caucasian Realm/Subrealm, East Pacific Realm/Subrealm (pre-Tithonian), Indo-Pacific or Austral Realm/Subrealm (Tithonian only)

Andean Province [An] *including Antofagusta Subprovince* [An(A)] and *Neuquén Subprovince* [An(N)] (western South America, Chile, Peru, Argentina, Antarctic Peninsula, Mexico). Jurassic ammonite faunas of the East Pacific region often show strong affinities with those of Tethys and especially those of the Submediterranean Province faunas, at least at generic level. At species level, however, genuine differences are apparent. During such intervals (Hettangian to Early Bajocian, mid-Callovian to ?Kimmeridgian), it is simplest to consider the former areas as part of a broad Mediterran–Caucasian Realm or Subrealm – the main connection between the two areas being the seaways of the Hispanic Corridor, between north and south America. From the Late Bajocian and through the Bathonian, however, links were interrupted sufficiently to allow a level of endemism to develop in the East Pacific, which Westermann (1981) considered to be of Realm status (although later demoted to a Subrealm by Hillebrandt *et al.* (1992a, b)). In the Tithonian, faunas from southern South America developed further distinctive characters at the specific and generic level, leading Enay & Cariou (1997, 1999) to propose an Austral Realm for ammonoids (although subsequently incorporated into the Indo-Pacific Realm or Subrealm by Westermann, 2000a, b). Nevertheless, although faunal affiliations changed through the Jurassic, the geography of a distinguishable 'Andean Province' did not.

During periods of good Tethyan links, distinction of the Andean Province is mainly at species level, although a few endemic genera do occur. In the Hettangian, pandemic genera of Psiloceratidae, Schlotheimiidae and Arietitidae are typical as in Mediterranean areas, but include some endemic species. Pliensbachian to Aalenian faunas repeat the pattern, with widespread genera including representatives of the Polymorphitidae, Hildoceratidae, Dactylioceratidae and Phymatoceratidae, but with some endemic species and genera, including *Atacamiceras* (Hildoceratidae) in the Toarcian, and *Puchenquia* and *Sphaerocoeloceras* (Phymatoceratidae) in the Aalenian. East Pacific *Fanninoceras* (Oxynoticeratidae) is also present in the Late Pliensbachian.

Virtually complete interruption of links with Mediterranean areas during the later Bajocian and Bathonian, however, led to the development of a separate East Pacific Realm or Subrealm when various endemic Stephanoceratoidea are typical – some of which are shared between the Andean Province and North Cordilleran areas. A differentiation between northern and southern Andean Province areas also began to develop at this time, and continued to the end of the Jurassic, despite changes in Realm-level faunal affinities. Northern, low latitude faunas are typically more diverse, with larger numbers of European-type Tethyan taxa – including Phylloceratina – which were rare or absent further south in mid-latitude areas. This character, combined with some limited endemism, distinguishes a low latitude Antofagusta from mid-latitude Neuquén 'subprovince' (Hillebrandt *et al.*, 1992a, b). In the Bajocian, the Antofagusta Subprovince is characterized by a variety of Stephanoceratidae, including several restricted genera, such as Andean *Duashnoceras* and East Pacific *Lupherites* and *Stephanosphinctes*, associated with some Mediterran–Caucasian Haploceratina and Perisphinctidae. Notably, Phylloceratina are recorded. Neuquén Subprovince faunas also include pandemic genera (of Sonninidae, Perisphinctidae and Stephanoceratidae) but include endemic *Chrondroemileia* (Otoitidae), again with East Pacific *Duashnoceras* (Stephanoceratidae) and *Megasphaeroceras* (Sphaeroceratidae). By the Bathonian, more endemic or restricted East Pacific Sphaeroceratidae had appeared (*Lilloetia*, *Xenocephalites* etc.), together with the first Reineckeiidae (restricted Andean *Neuquenicera*s). Typical Mediterran–Caucasian genera are also present. Neuquén Subprovince faunas are broadly similar, although endemic *Stehnocephalites* (Family Sphaeroceratidae) is also present and Phylloceratina appear to be absent. By the later Early Callovian, the distinctiveness of the East Pacific Realm had waned, although initially some typical, restricted Sphaeroceratidae (*Eurycephalites* and *Xenocephalites*) survived throughout the region. *Neuqueniceras* is present throughout Andean areas, although pandemic Mediterran–Caucasian genera are also present with most variety in

Antofagusta Subprovince areas. A few endemic forms include *Guerrericeras* (Family Oppeliidae).

In the Oxfordian, although pandemic Perisphinctidae are present throughout Andean areas and often assigned to European genera (‘*Perisphinctes*’ etc.), they are not the same and are endemic to at least species level. Neuquén areas also include endemic late Sphaeroceratidae (*Araucanites*) and some Aspidoceratidae. In the Antofagusta Subprovince, Cuban Province *Cubaspidoceras* (Aspidoceratidae) and endemic *Praeataxioceras* (Perisphinctidae) are recorded, together with pandemic Aspidoceratidae, Oppeliidae and Pachyceritidae. Although Kimmeridgian faunas do not appear to be well characterized in Andean areas, those of the Tithonian are characteristically rich, with many Ataxioceratidae, as well as Himalayitidae, Aspidoceratidae, Neocomitidae, Haploceratidae etc. throughout. Antofagusta Subprovince faunas, however, again show stronger Mediterran–Caucasian links than those to the south, although some endemic Ataxioceratidae and Oppeliidae may be present (*Mazapilites*, *Salinites*, *Aceredites*, etc.). Southern Neuquén Subprovince faunas, however, developed an Indo-Pacific/Austral character and include *Blandfordiceras* (Neocomitidae) and endemic *Windhauseniceras* (Himalayitidae).

Representative literature on the province includes: Enay & Cariou (1997, 1999), Hillebrandt (2000, 2006), Hillebrandt *et al.* (1992a, b), Riccardi *et al.* (1992), Salvador *et al.* (1992) and Westermann (1981).

Cuban Province [C] (Cuba, central America). The presence of endemic genera and species of Perisphinctidae and Haploceratoidea during the Oxfordian indicates the existence of the Cuban Province. The Province is probably also equivalent, at least in part, to the Caribbean Province of Enay (1980), which is recognizable in the Kimmeridgian and Tithonian. Mid-Oxfordian faunas are the most distinctive and include endemic *Vinalesphinctes* and *Cubasphinctes* (Perisphinctidae) and *Cubochetoceras* (Oppeliidae) apparently alongside Andean *Araucanites* (Sphaeroceratidae) and some Mediterran–Caucasian genera including certain Aspidoceratidae. In the Kimmeridgian, typical Mediterran–Cauacasian genera are also present, for instance in Mexico, alongside endemic *Pararasenia*, *Epicephalites* and *Procraspedites* (Perisphinctoidea). Tithonian faunas, however, appear to be very close to Andean but may contain endemic perisphinctoidean genera, according to Westermann (2000a, b). Representative literature on the province includes: Cecca (1999), Myczynski & Meléndez (1990) and Westermann (2000a, b).

Pan-Tethyan and Pan Boreal Superrealms

Mediterran–Caucasian Realm/Subrealm, East Pacific Realm/Subrealm and Boreal–Pacific Realm/Subrealm

Athabascan Province [At] (western North America), *Shoshonean Province/Subprovince* [S] (Western Interior of the USA) and *Northeast Pacific Province/Subprovince* [NE] (northwestern North America). Faunas of the North Cordilleran areas (*sensu* Westermann, 1981) show both Tethyan and Boreal influences and, from the Late Bajocian to the Early Callovian, share characteristic East Pacific Realm genera with the Andean Province. A distinct Athabascan Province was characteristic of much of the Jurassic history of the western USA and Canada, but the Shoshonean Province is known primarily from the Late Bajocian to the Oxfordian. The latter was characteristic of the restricted sea of the Western Interior of the USA. Although mainly an Early Cretaceous phenomenon (Page, 1996), the boreal, Northeast Pacific Province does appear to be recognizable in the Tithonian of NW Canada and adjoining areas.

Earliest Jurassic (Hettangian) Athabascan Province faunas include frequent Phyllo- and Lytoceratina, associated with Psiloceratidae, Schlotheimiidae and early Arietitidae, indicating clear Mediterran–Caucasian Province affinities. Endemic species are common, however, and some genera are virtually endemic, for instance *Mullerites* (Schlotheimiidae), *Sunrisites* (Arietitidae) and *Badouxia* (Psiloceratidae), which also ranges into the earliest Sinemurian. From the Sinemurian to the Aalenian, the pattern is similar, with typical pandemic Mediterran–Caucasian genera, including a few endemic species and a few endemic or restricted genera. The latter include *Arctoasteroceras* (Arietitidae) in the Late Sinemurian, *Fanninoceras* (Oxynoticeratidae) and *Pseudoskirroceras* (Eoderoceratidae) in the Late Pliensbachian and *Yakounia* in the Toarcian. In the Aalenian, however, only typical Mediterran–Caucasian Hildoceratidae and Phymatoceratidae genera seem to be present. With the development of the East Pacific Realm or Subrealm during the Bajocian, Athabascan faunas developed with a greater range of endemic genera, including *Alaskinia* (Sonninidae), *Pseudocidoceras* (Otoitidae), *Zemistephanus* (Stephanoceratidae), together with East Pacific *Megasphaeroceras* (Sphaeroceratidae) and *Lupherites* (Stephanoceratidae), associated with more typically Mediterran–Caucasian genera. Endemism increased into the Bathonian, with East Pacific Sphaeroceratidae (*Eurycephalites*, *Iniskinites* etc.) remaining important and associates including endemic *Parareineckeia* (Stephanoceratidae) and *Epizigzagiceras* (Pseudoperisphinctinae?). A few Mediterran–Caucasian Perisphinctidae and Tulitidae are also recorded but the presence of Indo-Pacific *Xenocephalites* (Sphaeroceratidae) and Arctic *Cranocephalites* (Cardioceratidae) and *Kepplerites* (Kosmoceratidae) is noteworthy. The presence of the latter two families in northern areas gradually reduced the distinctiveness of the Province and, by the Mid Callovian, with the disappearance of typical East Pacific Sphaeroceratidae such as *Eurycephalites*, Athabascan faunas (and the East Pacific Subrealm) became barely distinguishable.

The Shoshonean Province/Subprovince of the Bajocian and Bathonian is characterized by extremely low diversity, often monospecific faunas with little more, respectively, than endemic *Eocephalites* and *Paracephalites* (Sphaeroceratidae). In the Bathonian, early *Kepplerites* (Kosmoceratidae) are also present as endemic species. Boreal genera also occur in the northwestern USA in the Callovian and Oxfordian and a mixing with Tethyan-type genera sometimes creates a Subboreal style assemblage in those areas. The apparent absence of many typical European Boreal species, however, gives these faunas a Boreal–Pacific style and the recognition of a Northeast Pacific Province may be justifiable.

Representative literature on the province includes: Guex (1995), Hillebrandt *et al.* (1992a, b), Jakobs (1997), Poulton *et al.* (1992), Smith & Tipper (1996) and Westermann (1981).

Pan-Boreal Superrealm

Arctic Realm/Subrealm, Boreal–Atlantic Realm/Subrealm and Boreal–Pacific Realm/Subrealm

Arctic (or 'Boreal') Province [A] (Scotland, East Greenland, Spitzbergen, Siberia, Canadian Arctic, Alaska) and *Bering Province* [B] (North Pacific margin; Japan, northwestern North America, northeastern Siberia). Faunas of the Arctic Province were already distinct from the earliest Jurassic and are characterized by some of the lowest diversity of any in the Period, many being virtually monospecific. Distinction is initially mainly at species level but, from the Bajocian onwards, endemic genera become significant. The Bering Province occupied a marginal area in the Aalenian and Early Bajocian but did not extend far into the Boreal Sea. Faunas of the Province are characterized by a small number of endemic genera associated with more typical Arctic Province species.

During the Hettangian and Sinemurian, Arctic Province faunas are characteristically very low diversity and, as elsewhere, dominated by typical Psiloceratidae and Schlotheimiidae and, subsequently, Arietitidae. A number of endemic species appear to be present, however, in both the Hettangian and Sinemurian. Pliensbachian faunas are similar in style to those of the NW European Province, with Polymorphitidae, Liparoceratidae and Amaltheidae, but including endemic *Amaltheus* (*Nordamaltheus*). Toarcian faunas, however, contain more restricted elements, which although found at certain levels in neighbouring provinces, do seem to be most consistently recorded within the Arctic Province. These include a variety of genera of Hildoceratidae (*Tiltoniceras*, *Cleviceras*, *Pseudolioceras* etc.) and some later Dactylioceratidae. *Arctomercaticeras*, *Kedonoceras* and *Kolymoceras* (all Hildoceratidae) do seem to be true endemics. From the Late Toarcian to the Bajocian, virtually only *Pseudolioceras* (Hildoceratidae) is recorded.

From the Late Bajocian, characteristic Boreal Stephanoceratoidea developed and Bathonian Arctic Province faunas are already distinctive, with endemic early Cardioceratidae (*Cranocephalites*, *Arctocephalites* etc.) and early Kosmoceratidae (*Kepplerites*). Although barriers to migration to more southerly areas had broken down by the Callovian, this general character was maintained at high latitudes (Fig. 4) and Arctic faunas are dominated by Boreal Cardioceratidae until the Early Kimmeridgian, including endemic *Hoplocardioceras* towards the end of their range. Subboreal Province Aulacostephanidae are typically rare in the Oxfordian but become more abundant and characteristic in the Early Kimmeridgian. By the Late Kimmeridgian and into the Tithonian, Arctic faunas become dominated by low diversity faunas of Dorsoplanitidae, including genera typical of neighbouring Boreal–Atlantic areas. The Bering Province is essentially an Aalenian to Bajocian phenomenon and initially includes virtually monospecific faunas of endemic species of *Erycitoides*, although developing with endemic genera, most notably *Arkelloceras* (both Phymatoceratidae), in the Bajocian. The presence of Arctic *Cranocephalites* (Cardioceratidae) in the Bajocian is noteworthy.

Representative literature on the both provinces includes: Callomon (1985), Hillebrandt *et al.* (1992a, b), Poulton *et al.* (1992), Sey *et al.* (1992) and Westermann (1981, 2000b).

Boreal–Atlantic Realm/Subrealm

Subboreal Province [SB] (England, northern France, northern Germany, Poland, Russian Platform). The Province is first recognizable from the Late Pliensbachian to the earliest Late Toarcian, when direct connections between Tethyan and Boreal areas first opened up within Europe. Faunas are dominated firstly by late Liparoceratidae (*Pleuroceras*) and, subsequently, in the Toarcian, by Dactylioceratidae. Submediterranean Hildoceratinae and Harpoceratinae (both Hildoceratidae) are typically rare, but some genera appear to have a northern preference and are common at certain levels (*Tiltoniceras* and *Cleviceras* etc.).

During the Early Callovian, re-opening of migration allowed a new phase of mixing of previously separated Boreal and Tethyan Realm faunas and a clear latitudinal control of ammonite faunas emerged (Fig. 3). In the Callovian, Kosmoceratidae become characteristic but are replaced by Cardioceratidae in the latest Callovian and into the Oxfordian. Typical Tethyan, Submediterranean Province Perisphinctoidea and Oppeliidae may also be present, but generally in much smaller numbers. Late Oxfordian faunas of southern Britain are dominated by Perisphinctinae, with relatively few Cardioceratidae, and include species – and possibly genera – which are distinct from typical Submediterranean areas to the south (including species of *Perisphinctes* s.s.). It appears likely that these faunas characterize a separate subprovince, although further comparison with contemporaneous perisphinctid assemblages elsewhere is still required to determine an appropriate palaeobiogeographical affinity. By the later Oxfordian and into the Early Kimmeridgian, the largely endemic Aulacostephanidae appear alongside typical Cardioceratidae in Subboreal areas. In the Tithonian, however, the establishment of barriers to migration prevented interchange across Europe, and two Provinces become recognizable in former Subboreal areas: the East European and the West European (see below). Representative literature on the Province includes: Birkelund *et al.* (1983), Cariou *et al.* (1985, 1997), Dommergues *et al.* (1997), Page (1991, 2003, 2004a) and Thierry *et al.* (1997).

West European Province [WE] (England, northern France). During the latest Jurassic (Tithonian), reduced exchange between the western and eastern parts of the former Subboreal Province led to the development of ammonite faunas distinguishable largely in terms of the dominance of particular perisphinctoidean genera, but also including a number of endemic species. West European, Late Tithonian faunas are dominated by Dorsoplanitidae and characterize a 'Portlandian' (regional) Stage. Representative literature on the province includes: Cope (1967, 1978) and Wimbledon (1984).

East European Province [EE] (Russian Platform, northern Poland, Pechoraland, ?East Greenland). The East European Province developed in parallel with the West European Province during the Tithonian and is often distinguished within a 'Volgian' (regional) Stage. Virgatitidae and Dorsoplanitidae are characteristic, the latter including some genera rare or absent in the West European Province such as *Dorsoplanites*. Representative literature includes: Callomon & Birkelund (1982) and Krymholts *et al.* (1988).

4. CONCLUSIONS

Despite recent advances in the stratigraphical use of microfossil groups and non-palaeontological techniques, such as chemo- and magnetostratigraphy, the ammonites retain their pre-eminent position as the most reliable and accurate correlation tools available for marine Jurassic sequences. They have many other uses, however, and deserve to be recognized more widely for their value in more palaeontologically biased studies, such as palaeobiogeography, and of evolutionary mechanisms and patterns – including speciation and extinction. These latter studies, however, are often hindered by an incomplete understanding of the basic taxonomy, from species level upwards. This situation is exacerbated by a paucity of research funding as a result of a preference amongst most funding organizations for more esoteric or dramatic fossil groups and more fashionable, but scientifically often transient, theories and hypotheses. Where contemporary studies have been carried out, the ammonites continue to demonstrate their palaeontological value as the most characteristic and, arguably, the most generally geologically useful, marine fossil that the Jurassic System has to offer.

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