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Biogeographic differentiation of the Oxfordian and Early Kimmeridgian ammonite faunas of Europe, and its stratigraphic consequences

ABSTRACT: The Oxfordian and Early Kimmeridgian ammonite provincionalism, gradually arising through that time, makes it necessary to set up the separate zonal schemes for different parts of Europe. Besides the generally known differences in ammonite faunas between four distinct bioprovinces, there is a growing evidence that, beginning from the Middle Oxfordian, the ammonite faunas of the western part of the Submediterranean Province differ from those of the eastern part of this province. The two subprovinces, the Iberian-Aquitaine Subprovince and the German-Polish Subprovince, are thus recognized within the Submediterranean Province. The correlation of the Boreal and Subboreal zonal schemes with the Submediterranean one in the Upper Oxfordian and Lower Kimmeridgian is based on the invasions of Boreal ammonites of the genus *Amoeboceras* into the Submediterranean Province, and on the comparison of the evolutionary development of the family Aulacostephanidae in the Subboreal and Submediterranean Provinces. The successive migration waves of Boreal and Subboreal ammonites into the Submediterranean Province corresponded therein to the marked changes in ammonite faunas of Submediterranean/Mediterranean origin which could also be related with faunal invasions. These changes in ammonite faunas have possibly been controlled by transgressive impulses during the Late Oxfordian — Early Kimmeridgian in Europe.

INTRODUCTION

The ammonite differentiation in Europe during the Oxfordian and Early Kimmeridgian resulted in the development of four distinct bioprovinces, each of them characterized by different groups of ammonites. These were: the Boreal Province characterized by the Cardioceratidae, the Subboreal Province dominated by the Aulacostephanidae, as well as the Submediterranean and Mediterranean Provinces characterized by the Perisphinctidae, the Ataxioceratidae, the Aspidoceratidae, and the Haploceratacea, additionally with the abundant

Phylloceratáceae, the Lytoceratáceae, perisphinctids (*Passendorferia*, *Nebrodites*), and aspidoceratids (*Gregoryceras*) in the Mediterranean Province.

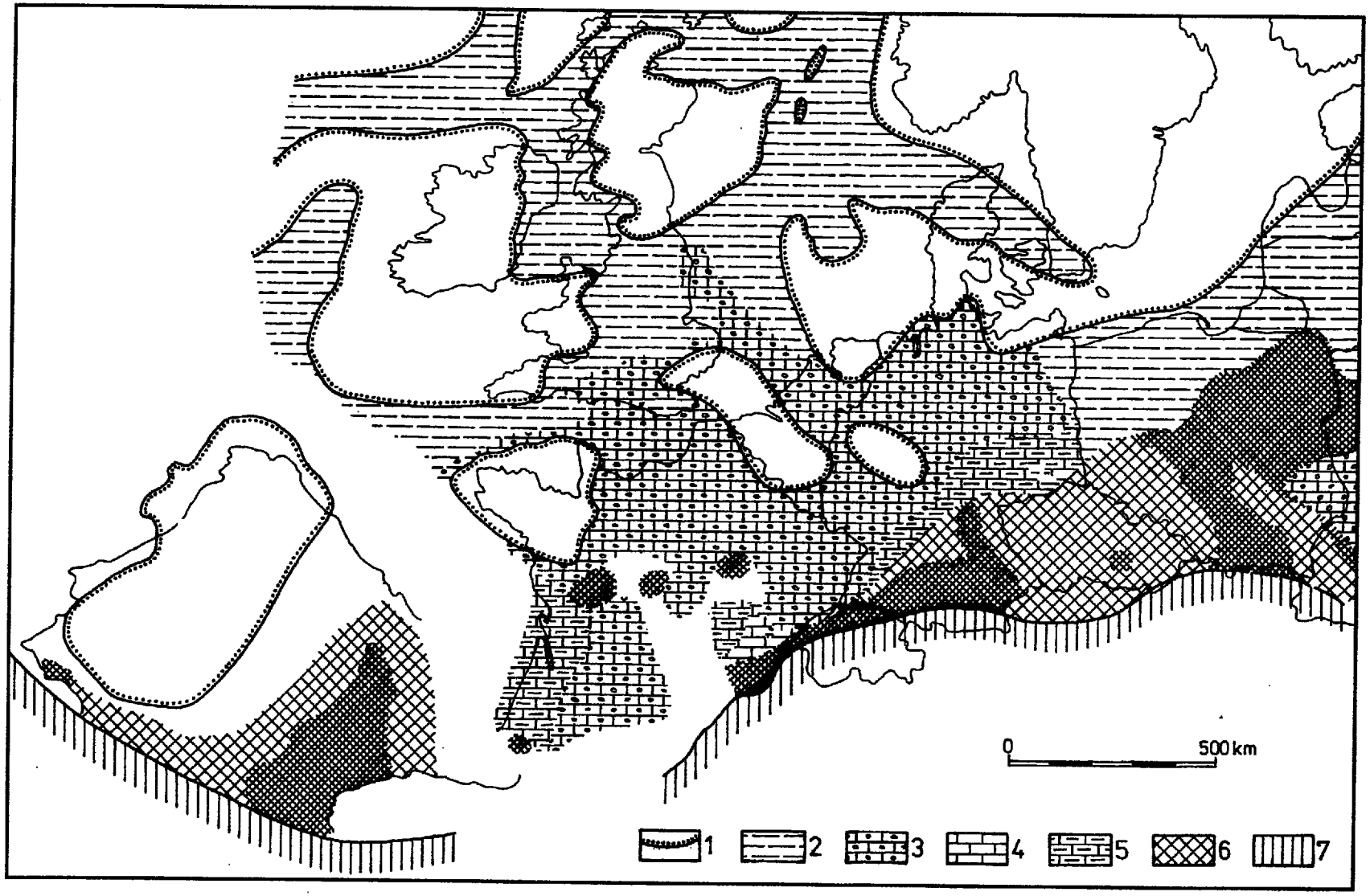
The existence of ammonite provincionalism necessitates the establishment of separate zonal schemes for the particular bioprovinces, the correlaton of which is sometimes troublesome. Fortunately, the marked overlapping of ammonite faunas of adjacent provinces have occurred from time to time giving strong clues for such correlation.

The changes in the biogeographic distribution of ammonite faunas may be explained by interaction of the geological agents and organic evolution (*cf. e.g.* BAYER & MCGHEE 1985). This can be demonstrated in studies of the Oxfordian and Early Kimmeridgian ammonite faunas in Europe.

EARLY OXFORDIAN TO EARLIEST MIDDLE OXFORDIAN BOREAL/TETHYAN AMMONITE ZONATION

The Boreal and Submediterranean ammonite faunas markedly overlapped in Europe during the Early Oxfordian and earliest Middle Oxfordian (early Plicatilis Chron, early Densiplicatum Chron). It was a consequence of a marked transgression which, at the beginning of the Callovian, opened the land-locked Boreal Sea and caused the "Boreal Spread" of the Cardioceratidae southwards. Its maximum was during the Early Oxfordian (ARKELL 1956, CALLOMON 1985, CARIOU & *al.* 1985). The Boreal ammonites of the genus *Cardioceras* reached as far southward as the northern Caucasus, the western Carpathians (down to the Czorsztyn Succession of the Pieniny Klippen Belt), and the southern Subalpine Chains of France. On the other hand, the Mediterranean/Submediterranean ammonites such as the Peltoceratinae, the Perisphinctinae, the Euaspidoceratinae, and the Haploceratáceae migrated northwards in abundance into NW European areas such as England and Scotland. This mingling of the Boreal and the Submediterranean/Mediterranean ammonite faunas produced the most marked faunal unification during Oxfordian — Early Kimmeridgian times which was observed over large part of Europe. The implication is that the standard Boreal ammonite zonation of the Lower Oxfordian and the lowermost Middle Oxfordian can be applied beyond the Boreal areas, in parts of the Submediterranean Province of Europe. It still lacks, however, an independent ammonite zonation for the Lower Oxfordian and lowermost Middle Oxfordian based on the Submediterranean/Mediterranean groups of ammonites which can be correlated precisely with the Boreal zonation. The ammonites of the subfamily Peltoceratinae which evolved very quickly in the Early Oxfordian and had a wide geographic distribution (MATYJA 1990) are possibly the most promising for construction of such a zonation. It should be remembered, that Boreal Cardioceratidae become rare southwards in the Submediterranean/Mediterranean Provinces, being completly unknown in southern Europe (*e.g.* in Spain, Italy, Balkan Peninsula). In all these areas, the detailed distinction of the Lower Oxfordian is impossible.

Paleogeography and facies during the Middle Oxfordian of Europe



1 — Areas of non-deposition and continental facies, 2 — siliciclastic facies (mainly shales, and locally siltstones and sandstones), 3 — shallow-marine carbonate facies, 4 — micritic limestone facies, 5 — marly facies, 6 — sponge megafacies (wider hatching indicates its possible original distribution), 7 — Tethyan facies

DIFFERENTIATION OF LATE MIDDLE — EARLY LATE OXFORDIAN AMMONITE FAUNAS OF THE SUBMEDITERRANEAN PROVINCE

The general northward retreat of the Boreal Cardioceratidae occurred during the late Middle Oxfordian an the early Late Oxfordian (*cf.* ARKELL 1956). It corresponds to the "*Cardioceras gap*" in the Submediterranean succession which is a stratigraphic interval where the Cardioceratidae do not occur or are rare; this interval covers a time span from the late Plicatilis Chron to the late Transversarium / early Bifurcatus Chrons. The nature of the Boreal retreat of the Cardioceratidae is complex. Initially, the Cardioceratidae became rare in the Submediterranean Province, whereas the Submediterranean ammonites of the genus *Perisphinctes* penetrated far northwards being abundantly known from the English Plicatilis Zone, and ranging as far as the Milne Land in East Greenland (CALLOMON 1960, CALLOMON & BIRKELUND 1980). This northward migration of Submediterranean ammonites was severely hampered during latest Middle Oxfordian — early Late Oxfordian due to a strong development of shallow-water carbonates in northern France and southern England. The shallow water areas, together with emergent Rinkøbing-Fyn High towards the East, very effectively limited faunal exchange between the Boreal Sea and the Submediterranean Sea of western Europe. The bordering zone represented a region of high environmental instability, where migration of ammonites was difficult, and where a special Subboreal ammonite fauna developed (FÜRSICH & SYKES 1977).

The Submediterranean Province in Europe occupied the areas of the Tethyan shelf, stretching from Portugal and eastern Iberian Chains to Dobruja, Crimea, and the northern Caucasus. The facies consisted of carbonates, mostly of deep-neritic sponge megafacies (LEINFELDER 1993, MATYJA & WIERZBOWSKI 1995; *see also* Text-fig. 1 herein), but fine-clastics facies were also formed in local basins.

When analysing the ammonite diversity within area as wide as the Submediterranean Province, one may recognize a great number of ammonite taxa of the genus and species level common throughout this territory. Nevertheless, there also existed some faunal differences between the western and eastern parts the province, with the boundary rather well marked between the Swiss Jura Mts and southern Germany. The perisphinctid genera such as *Larcheria*, *Neomorphoceras*, and the species e.g. *Perisphinctes nectobrigensis* MELÉNDEZ abundantly occurring in the Transversarium Zone of the western part of the Submediterranean Province (CARIOU & MELÉNDEZ 1990, MELÉNDEZ & FONTANA 1992) are almost completely unknown in its eastern part, where in a similar stratigraphic position occurs such indigenous taxon as *Subdiscosphinctes*. The consequence of these faunal differences is that the detailed subdivision of the Plicatilis and Transversarium Zones from the western part of the Submediterranean Province, partly based on local taxa (CARIOU & MELÉNDEZ 1990), cannot be fully applied in the eastern part of the province. A new

subdivision of the Plicatilis and Transversarium Zones based entirely on perisphinctid ammonites showing an extensive geographic distribution in the Submediterranean Province (MATYJA & GŁOWNIAK 1994) is of a wider applicability.

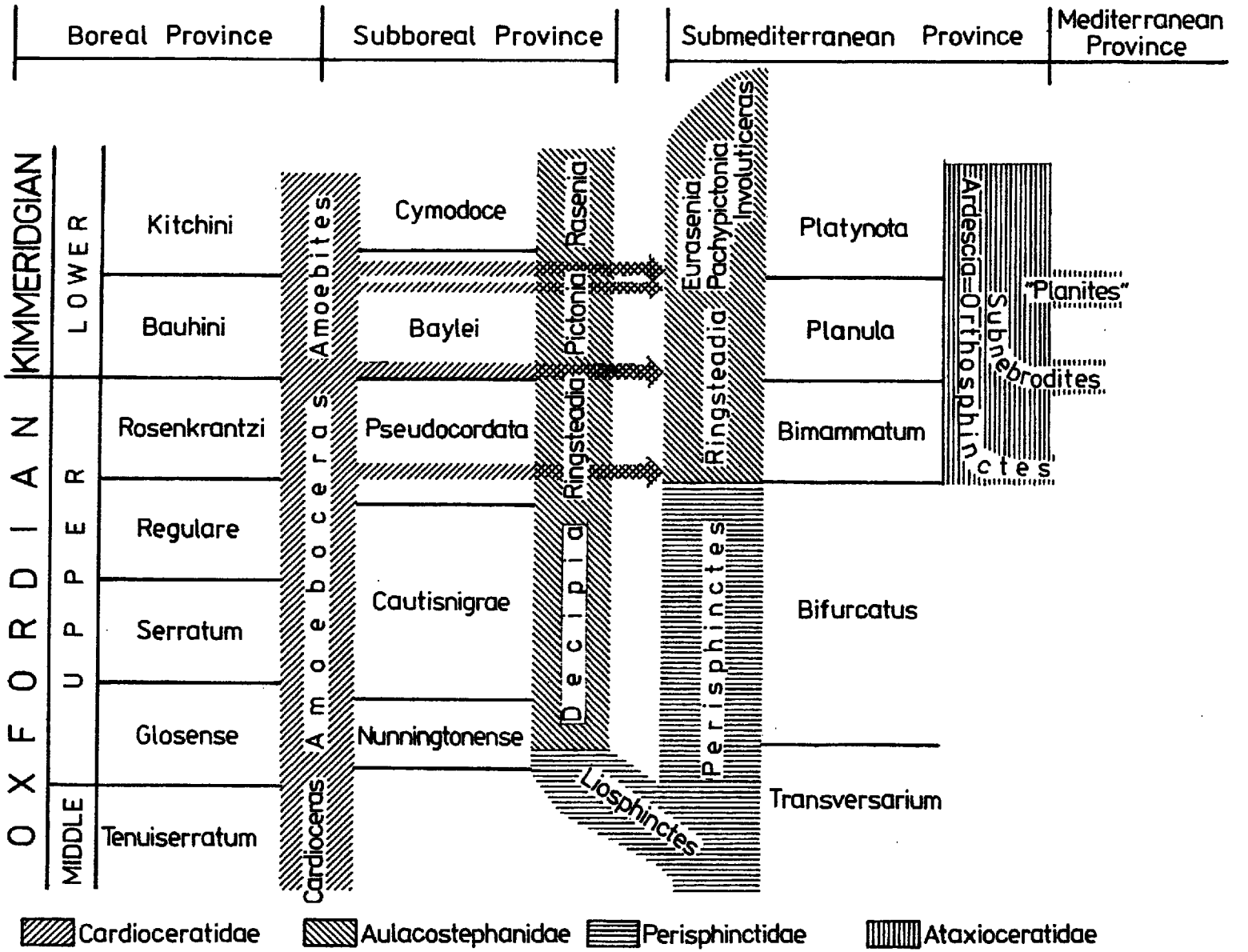
All this data suggest the necessity of recognizing the two subprovinces within the Submediterranean Province: the western — Iberian-Aquitaine Subprovince (or Atlantic Subprovince; *see* CARIOU & *al.* 1985), and the eastern — German-Polish Subprovince. The origin of these two subprovinces was possibly related with the strong development of shallow-water carbonate platform in the Swiss Jura Mts (*see* Text-fig. 1). This prograded markedly southwards during the Middle and Late Oxfordian (GYGI 1990) and made faunal exchange between western and eastern parts of the Submediterranean Province difficult. The East-to-West current circulation along the Tethys to Protoatlantic with a generally limited circulation on the northern Tethyan shelf (LEINFELDER 1993), emphasised the existing differences and favoured the development of ammonite provincialism, especially in the western part of the Submediterranean Province.

BIOGEOGRAPHY OF LATE OXFORDIAN — EARLY KIMMERIDGIAN AMMONITES OF THE FAMILIES CARDIOCERATIDAE AND AULACOSTEPHANIDAE

The ammonites of the families Cardioceratidae and Aulacostephanidae, although generally Boreal and Subboreal in character, showed considerable migrations southwards into the Submediterranean Province during the Late Oxfordian and Early Kimmeridgian (*see* Text-fig. 2). It is known, that the most active migration of the Subboreal and Boreal ammonites into the Submediterranean Province was possibly through the Peribaltic Depression in North-East Europe (WIERZBOWSKI 1991), but temporary migrations of the Subboreal Aulacostephanidae during the Early Kimmeridgian into the Aquitaine Basin also occurred (HANTZPERGUE 1988).

The genus *Decipia* of the early Late Oxfordian of NW Europe is the earliest form of the Aulacostephanidae with a root (*see* CALLOMON 1980) in the Submediterranean perisphinctids, such as *Liosphinctes*. The genus *Decipia* is virtually absent from Submediterranean Europe, which confirms its limited geographic distribution (*cf.* ENAY 1980). The origin of the family Aulacostephanidae marks the end of strong Submediterranean influences in NW Europe and the revival of the Subboreal Province, which had practically not existed there since Callovian times. This phenomenon approximatelly corresponds to the evolution of the genus *Cardioceras* into *Amoeboceras* in the Boreal Cardioceratidae lineage, a change which is treated as a convenient boundary of the Boreal Middle and Upper Oxfordian (SYKES & CALLOMON 1979). The same boundary in the Submediterranean Province can be traced in the upper part of the Transversarium Zone, where the last representatives of

Biogeographic differentiation and migrations of ammonite faunas during the Late Oxfordian and earliest Kimmeridgian in Europe



Cardioceras are immediately followed by the earliest *Amoeboceras*. The migration of the Boreal *Amoeboceras* into the Submediterranean Province during the late Transversarium Chron and early Bifurcatus Chron was, however, occasional, which precludes closer correlations in some parts of the corresponding stratigraphic interval (ATROPS & *al.* 1993, MATYJA & WIERZBOWSKI 1994).

The genus *Ringsteadia* is a direct descendant of the genus *Decipia* in the Subboreal Aulacostephanidae lineage. The appearance of *Ringsteadia* marks the base of the Pseudocordata Zone of the uppermost Subboreal/Boreal Oxfordian.

The oldest ammonites of the Subboreal genus *Ringsteadia* rarely appeared in the eastern part of the Submediterranean Province, in the late Bifurcatus Chron (SCHAIRER 1989). At the same time a migration of Boreal *Amoeboceras* also began. It was, however, the early Bimammatum Chron which brought the strong migration of *Ringsteadia-Amoeboceras* fauna into the eastern part of the Submediterranean Province (*see* Text-fig. 2), from Central Poland (with the celebrated *Amoeboceras* layer in the Semimammatum horizon) to southern Germany (*see* KLIEBERG 1981; MATYJA & WIERZBOWSKI 1988, 1994; WIERZBOWSKI 1991). This fauna has also been reported from the Swiss Jura Mts to south-eastern and eastern France (ENAY 1966, ATROPS & *al.* 1993), being almost completely unknown further West.

The discussed migration of the Subboreal/Boreal fauna strictly corresponds with the invasion of Mesogean/Mediterranean elements, such as the Ataxioceratidae, into shelf areas of the Submediterranean Province (ATROPS & MELÉNDEZ 1988). Both the Aulacostephanidae (genus *Ringsteadia* and its descendants), and the Ataxioceratidae (genus *Orthosphinctes* and its descendants) continously inhabited the Submediterranean Province after that time, and evolved there during the latest Oxfordian and Kimmeridgian. The former, however, inhabited mostly north-eastern parts of the province (German-Polish Subprovince), being rare or absent in its southern and south-western parts, except a few time intervals in the Early Kimmeridgian of Aquitaine.

The general succession of the *Ringsteadia* species in the Submediterranean Bimammatum Zone, and possibly the lowermost part of the Planula Zone, is very close to that of the Subboreal Pseudocordata Zone, which enables a closer correlation of the Submediterranean and Subboreal/Boreal zonal schemes. However, from the upper part of the Bimammatum Zone, and in the Planula Zone, there also appear ammonites of the genus *Ringsteadia* which differ from those of the Subboreal Province (WIERZBOWSKI 1970, 1991).

The genera *Pictonia* and *Rasenia* represent the succeeding members of the Subboreal Aulacostephanidae lineage. They evolved during the Baylei and Cymodoce Chrons, being characterized by very evolute and more heavily

ornamented shells in comparison with those of the older *Ringsteadia* genus (BIRKELUND & CALLOMON 1985). The appearance of the genus *Pictonia* marks the base of the Baylei Zone which is the boundary of the Oxfordian and Kimmeridgian in the Subboreal and Boreal zonal schemes.

The ammonites of the genus *Pictonia* are poorly known from the Submediterranean Province. The late ammonites of the genus *Ringsteadia* of the Planula Zone in Central Poland show, however, evolute coiling of inner whorls with the *Pictonia* stage of ornamentation consisting of variously accentuated ribs, and marked, sometimes even collared constrictions. These ammonites, although attributed to the genus *Ringsteadia*, are possibly (*see* WIERZBOWSKI 1994) the involute Submediterranean analogues of the true Subboreal *Pictonia*. The discussed ammonites are directly followed in the Submediterranean succession by ammonites of the genus *Rasenia*, attributed to the subgenera *Eurasenia*, *Pachypictonia*, and *Involuticeras*, and known from the upper Planula to the Divisum Zone. They mostly show discoidal shells with involute or weakly evolute coiling, not usually encountered in the Subboreal *Pictonia* and *Rasenia*.

The differences in evolutionary development of the Aulacostephanidae in the Subboreal and Submediterranean Provinces, from the early Baylei Chron, and approximately corresponding the Planula Chron, until the Cymodoce and Divisum Chrons, should be related with geographic variation which occurred in both areas. The achieved variation was represented at some stratigraphic levels, at least, as a continuous chain of intergrading subspecies with peripheral links different in morphology, but not necessarily with a fully completed process of speciation. This could explain, for example, the occurrence of some involute variants similar to the late Submediterranean *Ringsteadia* within the typical Subboreal *Pictonia* populations (BIRKELUND & CALLOMON 1985; *cf. also* GEYER 1961). Temporary stronger migrations probably smoothed the existing differences. All these suggest that the real taxonomic relations between the corresponding forms coming from the Subboreal and Submediterranean Provinces are of lower systematic rank than is usually accepted.

The Boreal ammonites of the genus *Amoeboceras* mostly appeared in the Submediterranean Province in successive migration waves during the latest Oxfordian and earliest Kimmeridgian (Text-fig. 2). Besides the discussed migration during the latest Bifurcatus — early Bimammatum Chrons, those so far recognized occurred at the turn of the Bimammatum and Planula Chrons, during the late Planula Chron (in the Galar Subchron), and the earliest Platynota Chron (ATROPS & *al.* 1993). These migrations give support for a closer correlation of the Boreal/Subboreal and Submediterranean zonal schemes; *i.a.* showing that the boundary of the Oxfordian and Kimmeridgian in the Submediterranean zonal scheme is drawn too high when compared with this boundary in the Subboreal subdivision (MATYJA & WIERZBOWSKI 1988). The successive Boreal *Amoeboceras* migrations into the Submediterranean Province

corresponded to the marked changes in ammonite faunas of the Submediterranean/Mediterranean origin which could also be related with faunal invasions (ATROPS & MELÉNDEZ 1988, 1994). The episodes of multidirectional ammonite migrations possibly correlate with transgressive impulses in the Late Oxfordian — Early Kimmeridgian basins of Europe (ATROPS & FERRY 1989).

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