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# Biological response of ammonites to changing environmental conditions: an example of Boreal *Amoeboceras* invasions into Submediterranean Province during Late Oxfordian

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ABSTRACT:

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*Amoeboceras* faunas constituting the typical element of the Boreal Province occur abundantly in two *Amoeboceras* layers in the Submediterranean Province ammonite succession of the Upper Oxfordian of Central Poland. When compared with those from the home-area of ammonites of the genus *Amoeboceras*, these invasive forms in the Submediterranean Province differ in their smaller shell-sizes, in the lack of differentiation of the shells into separate size-related morphs, and in the crowding of septa for up to one and a half whorls of the last part of the phragmocone. The densely-spaced septa appear at the beginning of the fifth whorl, after the "normally" septate inner whorls. This fits well with the beginning of the sexual cycle postulated for the phyletically related genus *Quenstedtoceras*. Such a long section of phragmocone with densely-spaced septa, indicating a prolonged period of low rate of shell growth, may be related to the attainment of a long period of sexual maturity due to environmental conditions untypical for Boreal forms.

**Key words:** ammonite ecology, ammonite reproductive cycle, ammonite invasion, palaeobiogeography, Jurassic, Oxfordian, Poland.

## INTRODUCTION

The Upper Oxfordian and Lower Kimmeridgian ammonite faunas in the area of epicratonic Poland are mostly of Submediterranean character, consisting principally of representatives of the families Oppeliidae, Ataxioceratidae and Aspidoceratidae, thus enabling easy recognition of the Submediterranean ammonite zonal scheme. This area, together with other areas of Europe, from Portugal to Dobruja, and the northern Caucasus, corresponding to the northern Tethyan shelf, constitutes the Submediterranean Province (*e.g.* MATYJA & WIERZBOWSKI 1995). A fairly uniform, but not very abundant, occurrence of ammonites of the family Aulacostephanidae, of Subboreal affinity, is recognised in some areas of the Submediterranean Province, including the territory of Central Poland. These ammonites appeared during the Late Oxfordian – Early Kimmeridgian in the Submediterranean Province, partly as newcomers from the Subboreal Province, and partly as forms which had already developed in the Submediterranean

Fig. 1. Syborowa Góra quarry: bedded limestones of the Hypselum Subzone, the *Amoeboceras* layer is indicated by an arrow

Province as the indigenous representatives of the family (MATYJA & WIERZBOWSKI 1995).

A mass spread of Subboreal ammonites of the family Aulacostephanidae toward the south during the Late Kimmeridgian changed the biogeographic position of the area of epicratonic Poland, placing it into the Subboreal Province, which results in the necessity of recognising of the Subboreal zonal scheme (KUTEK & ZEISS 1997, MATYJA & WIERZBOWSKI 2000).

Within the Upper Oxfordian and Kimmeridgian succession of Central Poland, a few thin horizons characterised by the common occurrence of Boreal ammonites of the genus *Amoeboceras* of the family Cardioceratidae are recognised. These so-called *Amoeboceras* layers mark short-term invasions of these Boreal ammonites (sometimes associated with other forms of Boreal/Subboreal affinity, such as bivalves of the genus *Buchia*), into the Submediterranean Province during the Late Oxfordian and Early Kimmeridgian, as well as into the Subboreal Province during the Late Kimmeridgian (*e.g.* MATYJA & WIERZBOWSKI 1988, 1997; KUTEK & ZEISS 1997). Such episodes of strong migration of the Boreal *Amoeboceras* have also been recognised in the other areas of the Submediterranean Province, in Germany, France, Switzerland (ATROPS 1982, ATROPS & *al.* 1993, SCHWEIGERT 1995, SCHWEIGERT & CALLOMON 1997), and in the Subboreal Province, in England (CALLOMON & *al.* 1971).

The Boreal ammonites of the genus *Amoeboceras* occurring in the *Amoeboceras* layers are represented almost exclusively by small forms that are usually interpreted as microconchs (*e.g.* CALLOMON 1988; MATYJA & WIERZBOWSKI 1988, ATROPS & *al.*1993). Detailed analysis of *Amoeboceras* from the two *Amoeboceras* layers of the Upper Oxfordian Bimammatum Zone of Central Poland has shown, however, marked abnormalities in shell development compared with that of the typical microconchs (MATYJA & WIERZBOWSKI 1999). This problem, and its biological consequences are discussed in detail below.

The *Amoeboceras* layers in the Bimammatum Zone in Central Poland are known from deposits of the sponge megafacies, which show a wide lateral extent from the massive limestones of the cyanobacteria-sponge bioherms to the bedded micritic limestones of wackestone to mudstone type of the surrounding basins. The *Amoeboceras* layers are generally thin, attaining about 15-40 centimetres in thickness. Their thickness, as well as lithology, including the microfacies character, do not appear to differ from that of the underlying and overlying beds (Text-fig. 1; see also MATYJA & WIERZBOWSKI 1997, Pl. 1, Fig. 1).

## STRATIGRAPHICAL POSITION OF THE *AMOEBOCERAS* LAYERS IN THE SUBMEDITERRANEAN BIMAMMATUM ZONE AND THEIR PALAEOGEOGRAPHICAL SIGNIFICANCE

Of the two *Amoeboceras* layers recognised within the Bimammatum Zone (Text-fig. 2), the lower one contains abundant representatives of the species *Amoeboceras ovale* (QUENSTEDT). The ammonites co-occur with the Boreal bivalve *Buchia concentrica* (SOWERBY) – see MATYJA & WIERZBOWSKI (1988, Pl. 1), as well as with numerous Submediterranean ammonites of the genera *Orthosphinctes*, *Euaspidoceras*, *Epipeltoceras* and *Taramelliceras*, and with Subboreal ammonites, such as *Microbiplices* and *Ringsteadia*. This lower *Amoeboceras* layer occurs in the semimmatum horizon of the Hypselum Subzone, and it is recognised in several sections both in the Cracow-Częstochowa-Wieluń Upland, and in the western border of the Holy Cross Mts. in Central Poland (MATYJA & WIERZBOWSKI 1988, Fig. 1). Moreover, common occurrence of *Amoeboceras ovale* (QUENSTEDT) may be traced at the same stratigraphical level in some other areas of the Submediterranean Province – in southern Germany, Switzerland, and southern France (ATROPS & *al.* 1993).

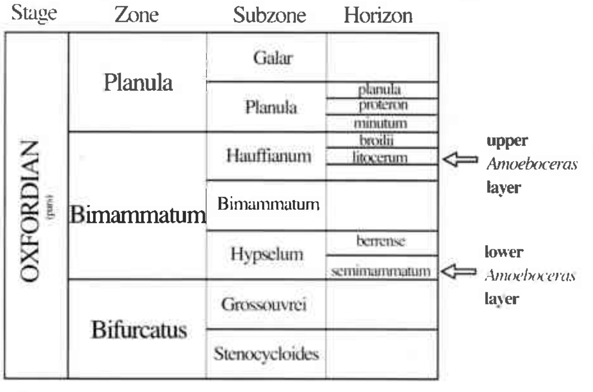


Fig. 2. Biostratigraphical position of the studied *Amoeboceras* layers in the framework of the standard Upper Oxfordian zonation of the Submediterranean Province

The level with abundant *Amoeboceras ovale* in the Submediterranean succession generally follows the marked turnover of ammonite faunas at the boundary of the Bifurcatus Zone, and the Bimammatum Zone. The beginning of the Bimammatum Chron brought a strong migration of ammonites of the family Ataxioceratidae (genus *Orthosphinctes*) of Mediterranean affinity, which replaced the representatives of the family Perisphinctidae existing earlier in the Submediterranean Province. On the other hand, the beginning of the Bimammatum Chron also shows the first appearance of Subboreal ammonites of the family Aulacostephanidae (of the *Microbiplices – Ringsteadia* group) in the studied area of the Submediterranean Province (MATYJA & WIERZBOWSKI 1995).

The upper *Amoeboceras* layer in the Bimammatum Zone (Text-fig. 2) yielded abundant representatives of the species *Amoeboceras bauhini* (OPPEL), represented by an assemblage of closely related morphotypes: *A. bauhini* (OPPEL) – *A. praebauhini* (SALFELD) – *A. lineatum* (QUENSTEDT). The ammonites co-occur with abundant Submediterranean ammonites, such as *Taramelliceras* (*Metahaploceras*), *Glochiceras* (*Coryceras*), and *Orthosphinctes*, but also with some of Subboreal affinity – especially *Pictonia densicostata* BUCKMAN (MATYJA & WIERZBOWSKI 1997, Pl. 5, Figs 5-11). The *Amoeboceras* layer lies in the Hauffianum Subzone, and it is easily recognisable in the sections of the Wieluń Upland in Central Poland (MATYJA & WIERZBOWSKI 1988, Fig. 1; MATYJA & WIERZBOWSKI 1997, Figs 1-2); the common occurrence of *Amoeboceras bauhini* is also recognised at the same stratigraphical level in other area of the Submediterranean Province – in southern Germany (SCHWEIGERT 1995, SCHWEIGERT & CALLOMON 1997).

The level with common occurrence of *A. bauhini* in the Submediterranean succession marks some other migration events, such as the above-mentioned appearance of Subboreal representatives of the genus *Pictonia* of the family Aulacostephanidae (MATYJA & WIERZBOWSKI 1997, see also SCHWEIGERT & CALLOMON 1997). These migration events possibly also include the sudden appearance, close to that level, of new forms of the family Ataxioceratidae of Mediterranean affinity, such as *Idoceras* (*Subnebrodites*), and their possible precursors (MATYJA & WIERZBOWSKI 1995).

The *Amoeboceras* layers of the Bimammatum Zone thus represent successive migration waves of

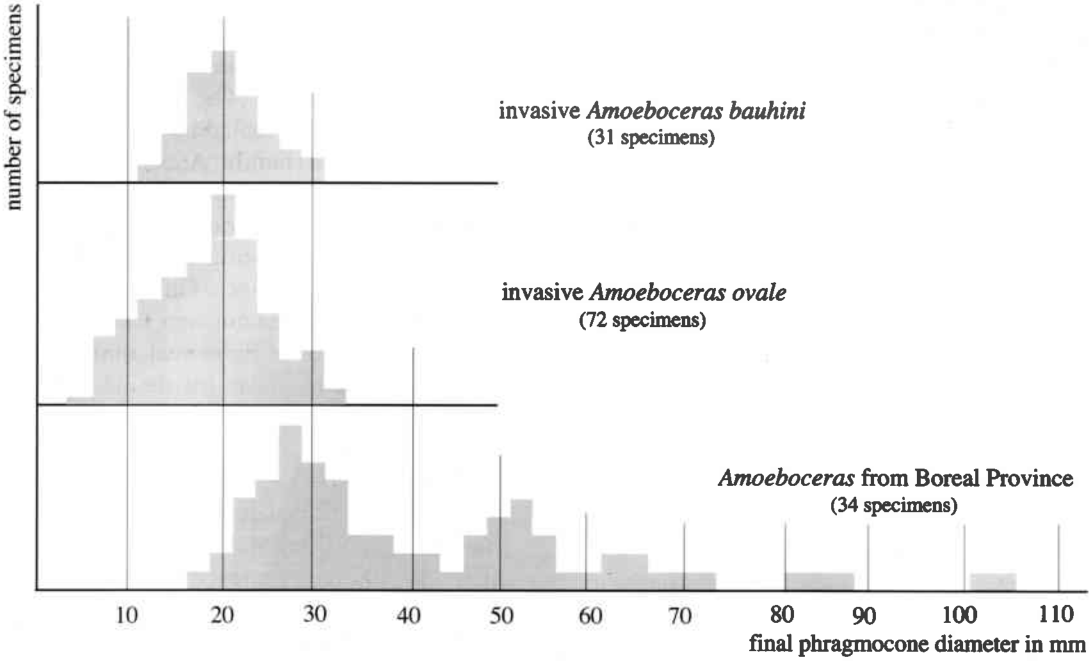


Fig. 3. Phragmocone diameters of the invasive *Amoeboceras* from the Submediterranean Province, and of the indigenous *Amoeboceras* from the Boreal Province

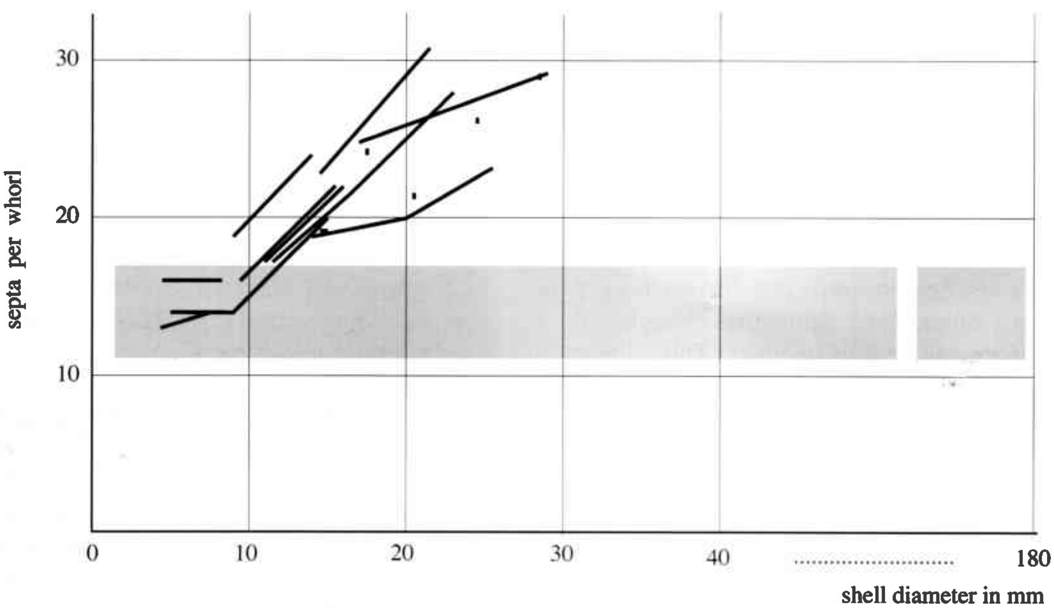


Fig. 4. Plot of septal density versus shell diameter in invasive *Amoeboceras*. Grey stripe indicates the "normal" septal density as observed at small diameters in invasive *Amoeboceras*, and up to large diameters in Boreal/Subboreal cardioceratids

the Boreal *Amoeboceras* into the Submediterranean Province. These layers also coincide with marked changes in other faunas of Subboreal and Submediterranean/Mediterranean origin, which could also be related to faunal invasions. This indicates that the intervals in the Submediterranean succession around the *Amoeboceras* layers correspond to multidirectional ammonite migrations, which could correlate with transgressive impulses during the Bimammatum Chron in the sedimentary basins of Europe (MATYJA & WIERZBOWSKI 1995, see also GYGI & *al.* 1998).

## PALAEONTOLOGICAL EVIDENCE OF THE AMOEBOCERAS FAUNAS

The specimens of the genus *Amoeboceras* from the two *Amoeboceras* layers are generally of small size. These of *Amoeboceras ovale* (QUENSTEDT), from the lower *Amoeboceras* layer, range in final diameter from 12 to 56 mm, whereas those of *A. bauhini* (OPPEL), including the morphotypes *A. bauhini – A. praebauhini – A. lineatum*, from the upper *Amoeboceras* layer, range from about 20 to 50 mm. In both species the ornamentation is generally of the isocostate type, but with slight modification at the end of the shell. In *A. ovale* the ornamentation consists of fairly numerous ribs strongly accentuated at the ventrolateral side of the whorls; the ribs are usually sharp, more regular on the inner whorls, and less distinct, somewhat irregular on the outer whorl; the keel is high, densely crenulated, and bordered by ventral sulci – for more detailed description see: MATYJA & WIERZBOWSKI (1988, pp. 423-424, Pl. 1), and ATROPS & *al.* (1993, pp. 216-218, Fig. 2; Pl. 1, Figs 9-13). In *A. bauhini* the ornamentation consists of fairly densely- to widely-spaced ribs with a marked tendency to develop a smooth spiral band on the whorl side; sometimes, more or less pronounced irregularities in ornamentation are observed on the outer whorl; the keel ranges from fairly high to low, markedly crenulated with poorly marked ventral sulci – for more detailed description see: MATYJA & WIERZBOWSKI (1988, pp. 424-426, Pl. 2), ATROPS & *al.* (1993, pp. 219-220, Fig. 2; Pl. 1, Figs 15-17), and MATYJA & WIERZBOWSKI (1997, Pl. 5, Figs 1-4).

The final diameter of the phragmocone, shown by increased septal density, is used for comparison of shell size in this study: it is a more convenient parameter than the final diameter of the shell, which is often difficult to recognise unequivocally. Detailed measurements were taken of specimens of *Amoeboceras ovale* (QUENSTEDT) from bedded limestones from several outcrops (MATYJA & WIERZBOWSKI 1988, Fig. 1) and from the massive limestones that crop out at Olsztyn near Częstochowa; as well of specimens of *Amoeboceras bauhini* (OPPEL) from the bedded limestones near Raciszyn (MATYJA & WIERZBOWSKI 1997, Fig. 2).

The range of shell diameters, measured at the final phragmocone/body chamber boundary of the specimens of *A. ovale*, is continuous from 7.6 mm to 32 mm, with the maximum at 20 mm (Text-fig. 3). The relevant measurements for *A. bauhini* also show continuous variation in final phragmocone diameters from 14 mm to 28.5 mm, with the maximum at 20 mm.

The ammonites of the genus *Amoeboceras* from the Upper Oxfordian of the Boreal/Subboreal provinces differ from the specimens studied, mostly in the existence of morphologically well defined micro- and macroconchs. The microconchs are small-sized isocostate forms, and the macroconchs are large, variocostate forms with nearly smooth last whorls (*e.g.* SYKES & CALLOMON 1979, MESEZHNIKOV & *al.* 1989). The range of shell size at the phragmocone/body chamber boundary calculated from illustrated and fully grown specimens from the Boreal Province (Text-fig. 3, see SYKES & CALLOMON 1979) shows a discontinuous spectrum from 18 mm to 103 mm, with two marked peaks at 27 mm, and 52 mm. The specimens from the *Amoeboceras* layers of the Submediterranean Province showing one size-class only, and generally with ornamentation of the isocostate type, may thus be compared with the microconchs of the Boreal/Subboreal forms. The occurrence of a single morph only in a considerable area of the Submediterranean Province is a remarkable phenomenon, which has been discussed in the palaeontological literature and treated as an argument for the existence of developmental polymorphism within the ammonites (MATYJA 1986, pp. 48-49; *cf.* also CALLOMON 1988).

There is some difference, however, in the full range of the final phragmocone diameters between microconchs from the Boreal/Subboreal provinces, and the specimens from the *Amoeboceras* layers (Text-fig. 3): the latter are statistically of smaller sizes. It is difficult to find a satisfactory explanation for this difference: it may result from various ammonitella sizes in the two groups of ammonites, but it may reflect the process of progenesis involving the invasive forms from the *Amoeboceras* layers.

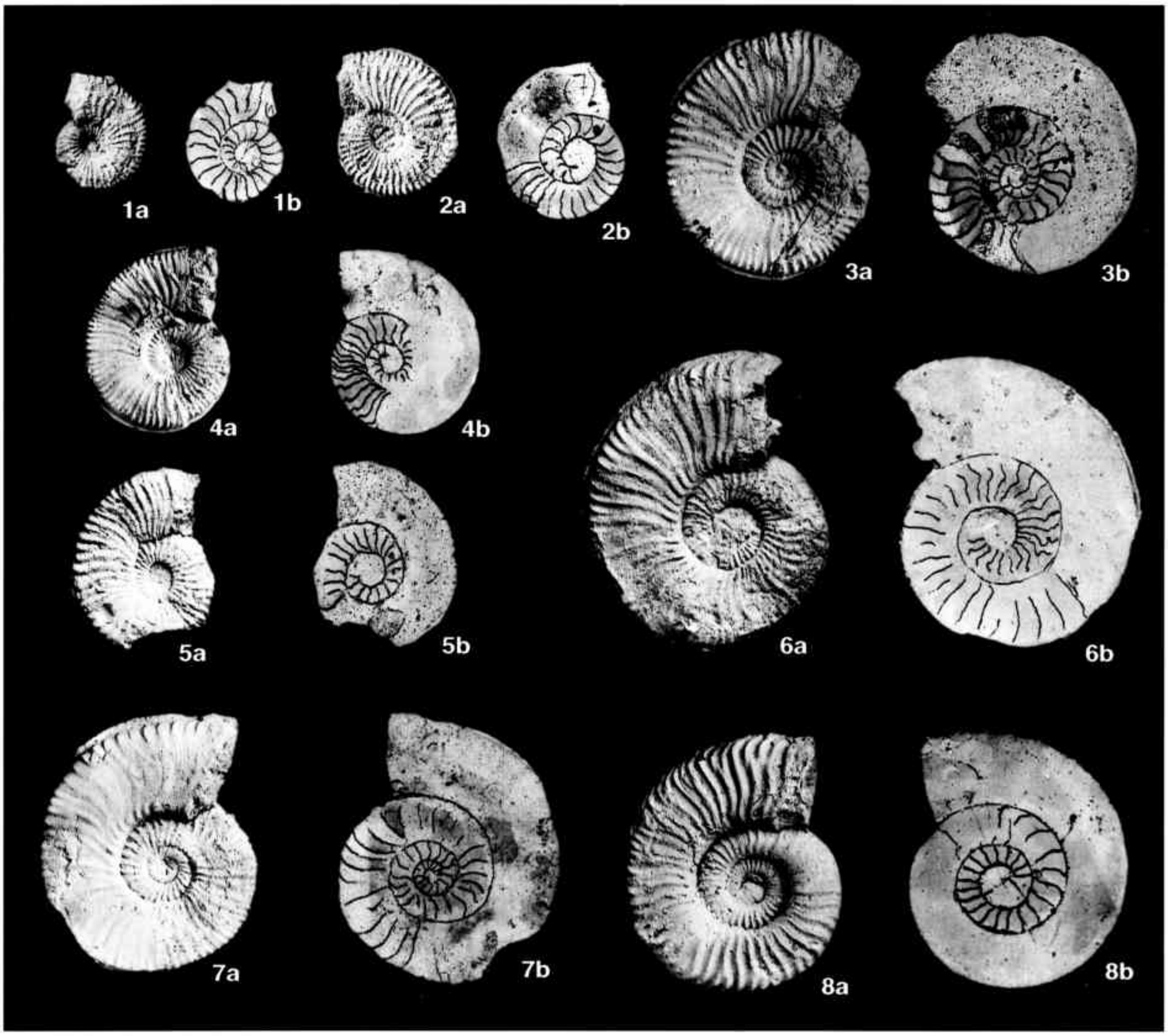


Fig. 5. *Amoeboceras* from the *Amoeboceras* layers in the Cracow – Wieluń Upland (a – lateral view of a shell, b – medial longitudinal section to show septal spacing); **1-7** *Amoeboceras ovale* (QUENSTEDT): bedded limestones, Hypselum Subzone; 1, 6, 7 – Syborowa Góra quarry; 2, 4 – Jaroszów quarry; 3 – Biskupice quarry; 5 – Biała Dolna quarry; **8** – *Amoeboceras bauhini* (OPPEL) – *A. praebauhini* (SALFELD) morphotype: bedded limestones, Hauffianum Subzone, Raciszyn quarry; all figures natural size

The principal difference between the microconchs of the genus *Amoeboceras* from the Boreal/Subboreal provinces and the specimens from the *Amoeboceras* layers is in the septal density. The pattern of septal density in the specimens from the *Amoeboceras* layers is observed after polishing one side of the shell down to the median line. The septa are often preserved, especially in the outer whorls of the phragmocone, but in some specimens they may also be observed in the inner whorls down to the ammonitella stage (Text-figs 4 and 5; see also MATYJA & WIERZBOWSKI 1999). The ammonitella has been recognised in some better preserved specimens of *A. ovale* from the massive limestones: it is fairly small, about 0.7-0.8 mm in diameter. The whorls following the ammonitella – up to the fourth whorl (the first one is the ammonitella itself), show rather widely-spaced septa, between 11-17 (mostly 13-14) septa per whorl. Then, from the beginning of the fifth whorl (which corresponds to a shell diameter between 7.6 and 9.3 mm), the septa become crowded. Except for the small specimens, which show only a few approximated septa at the end of the phragmocone, the commonly encountered larger specimens show a marked crowding of the septa, covering from three quarters of a whorl up to one and a quarter whorls, with 26 to 31 septa per whorl. The body chamber of the studied specimens is usually 7/8 of a whorl long, and the total length of specimens showing a different number of crowded septa is from five to six and a quarter whorls. The observed change in septal density from widely-spaced septa of the inner whorls to densely-spaced septa of the outer part of the phragmocone, is related to a corresponding change in ornamentation: from sharper and more regular ornamentation of the inner whorls, to less distinct, somewhat irregular ornamentation of the outer part of the shell. The special septal development, with a long sector of the shell being characterised by the occurrence of crowded septa, is recognised only in the specimens of *Amoeboceras* from the *Amoeboceras* layers, both in *A. ovale* and *A. bauhini*, but it is never observed in specimens of other genera occurring in the same layers. All these other ammonites, such as representatives of the genera *Orthosphinctes* and *Euaspidoceras* of Submediterranean/Mediterranean affinity, as well as ammonites of the *Microbiplices* – *Ringsteadia* group of Subboreal affinity, show about 14 septa per whorl, with a few last crowded septa observed at the end of the final phragmocone. Moreover, these forms are represented usually by more than one-sized morphs, interpreted usually as corresponding micro- and macroconchs, *e.g.* *Microbiplices* (m) – *Ringsteadia* (M.), *Orthosphinctes* (m) – *Pseudorthosphinctes* (M).

## BIOLOGICAL AND ECOLOGICAL INTERPRETATION OF THE STUDIED AMOEBOCERAS FAUNAS

The septal density during the ontogeny of ammonites is usually regarded as corresponding to the growth rate of the shell (*e.g.* KULICKI 1974, MATYJA 1986, DOMMERGUES 1988), and thus related to biological and/or environmental factors. For the biological interpretation of the special septal pattern recognised in the *Amoeboceras* specimens from the *Amoeboceras* layers, detailed study of the development of ammonite shells based on extremely well preserved specimens of the genus *Quenstedtoceras* from the Łuków locality in eastern Poland is of special importance (KULICKI 1974). Firstly, there is a close affinity between the genera *Quenstedtoceras* and *Amoeboceras*, which are evolutionarily linked by the genus *Cardioceras*, forming the main lineage of the family Cardioceratidae during the latest Callovian, Oxfordian, and Kimmeridgian (CALLOMON 1985). But even more important for the interpretation of the special septal pattern in the studied *Amoeboceras*, is the recognition in shells of *Quenstedtoceras* of relative changes in septal density expressed by the value of the median angle between particular septa: such subtle approximations of septa include the first two approximations, connected with the embryonic development of the shells, and the following three approximations, which are already related to the reproductive cycle (KULICKI 1974). The last three approximations of septa, located between the fourth and the fifth whorl, between the fifth and the sixth and a half whorl, and at the seventh whorl respectively, have been interpreted as corresponding to successive phases of the reproductive cycle in terms of the theory of sexual dimorphism, and related to the male and female specimens separately, *i.e.* to the micro- and the macroconchs (KULICKI 1974, Fig. 8). According to MATYJA (1986) the last three approximations of septa corresponding to successive phases of the reproductive cycle, are related not to separate sexual forms, but to the existence of three morphs: the mini-, the micro-, and the macroconchs, recognised also in the genus *Quenstedtoceras*, according to the theory of the developmental polymorphism.

When counting the number of septa per whorl, it appears that their numbers in successive whorls in specimens of *Quenstedtoceras* from the Łuków locality are fairly constant and change over a small interval from 11 to 17 septa per whorl (Text-fig. 4). Such "normal" septal density may also be observed in ammonites of the genus *Amoeboceras* from the Boreal/Subboreal provinces, as inferred from specimens illustrated by SYKES & CALLOMON (1979), and MESEZHNIKOV & *al.* (1989). It should be remembered that in this way of counting the septa, their subtle approximations (*cf.* KULICKI 1974) also lie within a zone of "normal" septal density.

The studied specimens of *Amoeboceras* from the *Amoeboceras* layers in Central Poland show a two-phase development of the shells marked by different septal density (Text-fig. 4). The "normal" septal density is observed up to a shell diameter of 7.6 mm to 9.3 mm, which corresponds to about four whorls, after which the common occurrence of densely-spaced septa is seen. This change in septal density corresponds well to the beginning of the reproductive cycle as interpreted by KULICKI (1974) in the shells of *Quenstedtoceras* from the Łuków locality. Hence, the commonly observed crowding of septa recognised in both groups of studied *Amoeboceras* (*i.e.* in *A. ovale* from the lower *Amoeboceras* layer,

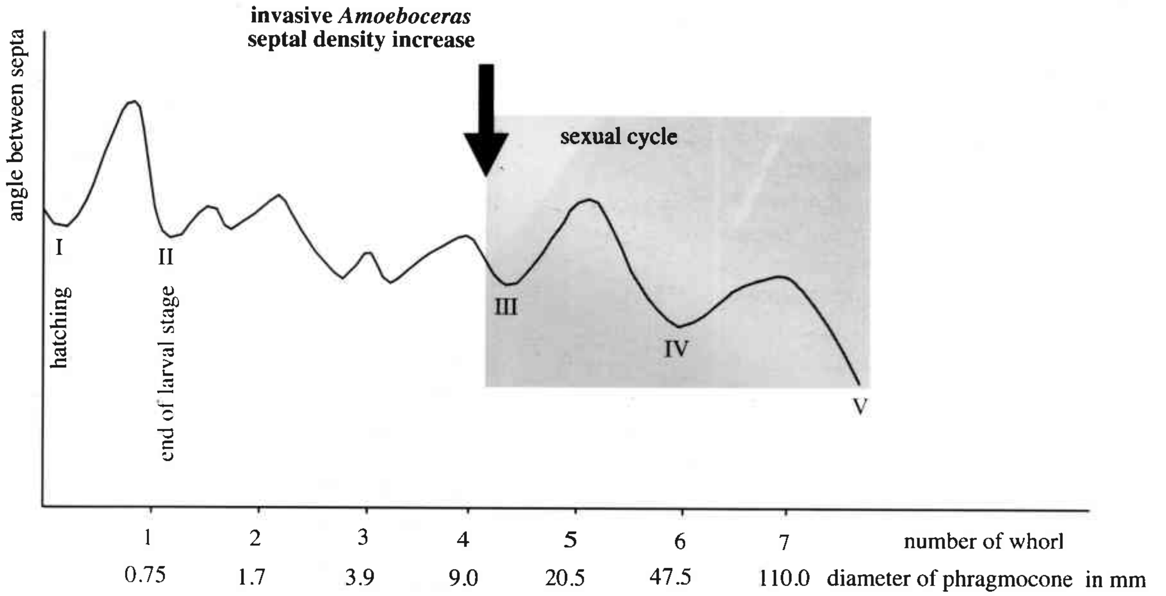


Fig. 6. Plot of septal spacing versus shell diameter (and corresponding number of whorls) in *Quenstedtoceras* from the Łuków locality, showing successive approximations of septa, and their interpretation *after* KULICKI (1974)

and in *A. bauhini* from the upper *Amoeboceras* layer) we interpret in a similar way, as being related to the attainment of sexual maturity.

The depositional environment of the Submediterranean Province which was reached by the Boreal ammonites of the genus *Amoeboceras* during their southward migration, was, in contrast to that of the Boreal Province, dominated by carbonate sedimentation. The Submediterranean ammonites occurring in the *Amoeboceras* layers do not show any special features that distinguish them from ammonites of the same affinity encountered in older and younger deposits in the sections studied. Furthermore, the lithology of the *Amoeboceras* layers, including their microfacies character, does not differ at all from that of the underlying and overlying beds. Thus, we interpret the special modifications of the shells of the genus *Amoeboceras*, recognised only in the *Amoeboceras* layers, as an adaptive reaction of these invasive forms to new environmental conditions.

Favorable conditions of environment may influence the ontogenetic development of cephalopods resulting in their earlier maturity: it is the case of *Nautilus* in aquaria which under such circumstances develops as abnormally small adults exhibiting "full mature modifications, including septal approximation and thickening" (see LANDMAN 1988). The low rate of shell growth shown by densely spaced septa may be considered to be related to a deficit of the energy required for building a shell: this could be constrained by limiting resources in the environment (*e.g.* BOLETZKY & WIEDMANN 1978, BUCHER & *al.* 1996), or by re-allocation of the existing resources to reproduction (KOZŁOWSKI 1992, STEARNS 1992). As the increase in septal density in the *Amoeboceras* from the *Amoeboceras* layers is observed after "normal" septal spacing up to the end of the fourth whorl (Text-fig. 6), which corresponds to the beginning of the reproductive cycle, we think that all the abnormal development of the shell characterised by its very low growth rate, resulted from the attainment of a prolonged stage of sexual maturity.

The ammonites of the genus *Amoeboceras* in their home-area, *i.e.* in the Boreal Province, showed particular phases of the reproductive cycle, separated by periods of normal shell development, which was possibly controlled by seasonality of the environment. On the other hand, in the case of the *Amoeboceras* layers in the Submediterranean Province, the existing seasonality was only fully "recognised" by the Submediterranean, as well as by some of the Subboreal ammonites, and it was not "noticed" by the invasive *Amoeboceras*, which consequently disturbed their development. Some special environmental conditions which could have influenced the development of ammonites in a similar way, may be suggested, for example, as an explana-

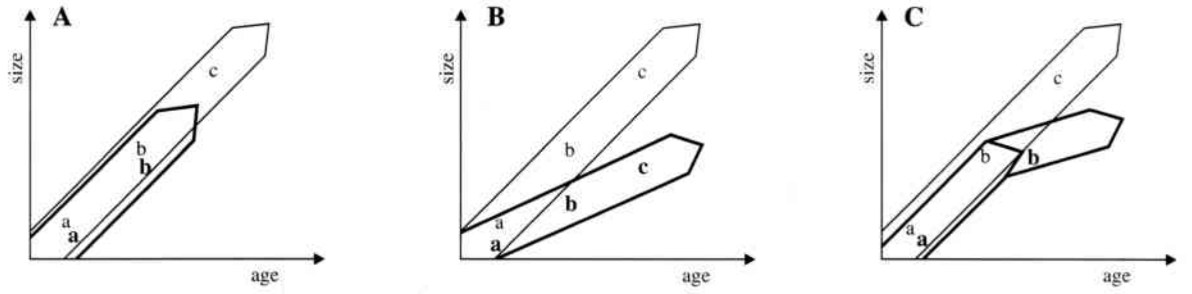


Fig. 7. The discussed cases of heterochrony (*modified after* MATYJA 1986); on the graphs, the normal ontogenetic development is marked by thin lines and symbols, whereas the various forms of heterochronic development are marked by thick lines and symbols; **A – progenesis**: the rates of growth and morphological transformation (individual stages marked by a-c symbols) are the same in both forms; the progenetic form, however, reaches its maturity (arrow-like end-point of the bars) earlier: hence, it is characterised by shorter longevity (measured as the projection of bars on the age axis), smaller final size, and an earlier morphological stage at maturity; **B – dwarfism**: the rate of morphological transformation, the moment of final maturation, and the longevity are identical in both forms; the growth rate of the dwarfed form, however, is lower: hence, the slope of the thick bar is less steep; **C – progenesis succeeded by "dwarfism"**: it is the case of the studied invasive *Amoeboceras* and is described in the text

tion for the small-sized ("dwarfed") ammonites of the Jurassic of Sicily possibly living in fissures opened in the sea-bottom (WENDT 1971), as well as those recognised in some parts of the *Polyplocus Schichten* (Valanginian) in north-west Germany (VOGEL 1959).

Of the heterochronic terms used in the literature (GOULD 1977, MCNAMARA 1986, MCKINNEY 1988) no one is strictly relevant to the studied case. When compared with *Amoeboceras* from the Boreal Province, discussed invasive forms from the Submediterranean Province are undoubtedly progenetic (Text-fig. 7A). The studied case, however, involves not only the progenetic relation between micro- and macroconchs, but possibly also the same relation between the two groups of microconchs (Text-fig. 3): the difference in final diameters of phragmocons between the microconchs from both areas suggests, that the maturity is attained earlier by the invasive forms. Next stage of ontogenetic development, marked by the occurrence of long sector of the shell with crowded septa, appearing in invasive *Amoeboceras*, may tentatively be classified as "dwarfism" (Text-fig. 7C). This only affects the advanced stage of growth, after beginning of the reproductive cycle. Some doubts concerning the classification of the described process as dwarfism (Text-fig. 7B) result from the lack in the invasive forms of morphological characters typical for advanced stages of adult macroconchs, such as the smooth last whorl.

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