

Oyster-bioimmured ammonites from the Upper Albian of Annopol, Poland: stratigraphic and palaeobiogeographic implications

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ABSTRACT:

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Ammonites *Mortoniceras* (*Subschloenbachia*) sp. are preserved as attachment scars on the oyster shells from the topmost portion of the Albian succession at Annopol, Poland. These oyster-bioimmured ammonites show a closest affinity to the representatives of *Mortoniceras* (*Subschloenbachia*) characteristic of the upper Upper Albian *Mortoniceras perinflatum* Zone. No ammonites indicative of the uppermost Albian–lowermost Cenomanian *Praeschloenbachia briacensis* Zone are recorded. Thus, the hiatus at the Albian–Cenomanian boundary at Annopol embraces the latter zone. The presence (and dominance) of *Mortoniceras* in the upper Upper Albian ammonite assemblage of Annopol suggests that the representatives of this Tethyan genus could migrate into the epicratonic areas of Poland directly from the Tethyan Realm, *via* the Lwów (Lviv) region.

Key words: Bioimmuration; Oysters; Ammonites; Albian; Cretaceous; Annopol; Poland; Stratigraphy; Palaeobiogeography.

INTRODUCTION

Mollusks with unstable aragonitic shells are lacking in many fossil assemblages, having been dissolved at various stages of diagenesis. However, the replicas of these shells may be preserved as a result of bioimmuration (Taylor 1990) by calcitic-shelled epibionts. A typical example is provided by ammonites preserved as attachment scars on the oyster left valves, and as xenomorphic (Stenzel 1971) replicas on the right (unattached) valves

of these bivalves. Such oyster-bioimmured specimens may be the only evidence of the presence of ammonites in beds where other remains of these cephalopods are absent (e.g., Kennedy 1971; Levy 1972).

In the present paper, the ammonites preserved on the bioimmuring oysters are reported for the first time from the upper Upper Albian phosphorite-bearing deposits exposed at Annopol, Poland. The interest of this material lies in the fact that it provides new data on the taxonomic composition, stratigraphy and palaeobiogeogra-

phy of the Albian ammonite faunas of Poland, so successfully explored by the late Ryszard Marcinowski (e.g., Marcinowski and Wiedmann 1985, 1990; Marcinowski and Radwański 1983, 1989; Kutek and Marcinowski 1996).

GEOLOGIC BACKGROUND

The mid-Cretaceous (uppermost lower Albian–lower Turonian) phosphorite-bearing succession is exposed around the town of Annopol, along the limbs of a small anticline (Annopol anticline, Rachów anticline in earlier publications; see Samsonowicz 1925, 1934; Pożaryski 1947; Cieśliński 1959, 1976). The Annopol anticline is located on the right bank of the Wisła (Vistula) river, Poland (Text-fig. 1A–C).

The Cretaceous strata of the Annopol anticline rest with a slight angular unconformity on an Upper Jurassic (Kimmeridgian) substrate (Samsonowicz 1925, 1934; Walaszczyk 1984). Their lithology was described in detail by Samsonowicz (1925; 1934), Pożaryski (1947), Cieśliński (1959), and Walaszczyk (1984, 1987). Stratigraphy is based mainly on the ammonites, inoceramid bivalves and foraminifers (Samsonowicz 1925; 1934; Pożaryski 1947; Cieśliński 1959, 1987; Marcinowski 1980; Marcinowski and Wiedmann 1985, 1990; Marcinowski and Radwański 1989; Marcinowski and Walaszczyk 1985; Walaszczyk 1987, 1992; Peryt 1983).

As far as the biostratigraphy of the Annopol succession is concerned, it should be noted that the *Hoplites (Hoplites) eodentatus* Subzone identified in the lower part of the Annopol succession (in the ammonite material from a sandstone at the bottom of the unit 1 in Text-fig. 1A) by Marcinowski and Wiedmann (1985, 1990) was regarded by these authors as the lowermost subdivision of the lower Middle Albian *Hoplites dentatus* Zone. Subsequently, this interval has been renamed as the *Pseudosonneratia steinmanni* Subzone and placed within the upper Lower Albian *Otohoplites auritifformis* Zone (e.g., Owen 2007, 2012; see Table 1).

The Albian–Lower Turonian succession at Annopol records the early phases of the great Cretaceous transgression (Hancock and Kauffman 1979; Marcinowski and Radwański 1983; Walaszczyk 1987) and is extremely thin (condensed) in relation to coeval strata in adjacent areas owing to its location on a submarine swell (Cieśliński 1976). In accordance with a simple transgressive–regressive model proposed by Juignet (1980) and Hancock (1990, 1993, 2004), the Annopol succession is interpreted as a series of thin transgressive units, truncated by layers of reworked phosphatic nodules and clasts, hard-

grounds and burrowed omission or erosional surfaces, which reflect a series of regression maxima (Text-fig. 1A).

THE AMMONITE-BEARING UNIT

The oyster-bioimmured ammonites studied came from the so-called Phosphorite Bed at the top of the Albian portion of the Annopol succession (Samsonowicz 1925, 1934; Radwański 1968; Marcinowski and Radwański 1983, 1989). These authors divided their Phosphorite Bed into the lower and upper part (e.g., Marcinowski and Radwański, 1983, fig. 6; Text-fig. 1A, C). However, what was called the Phosphorite Bed is better interpreted as two independent phosphorite beds terminating two separate transgressive–regressive units (third-order sequence stratigraphy cycles, numbered 2 and 3 in Text-fig. 1A, C). In terms of this new subdivision, the oyster-bioimmured ammonites were found in unit 3, in its middle portion (arrowed in Text-fig. 1A).

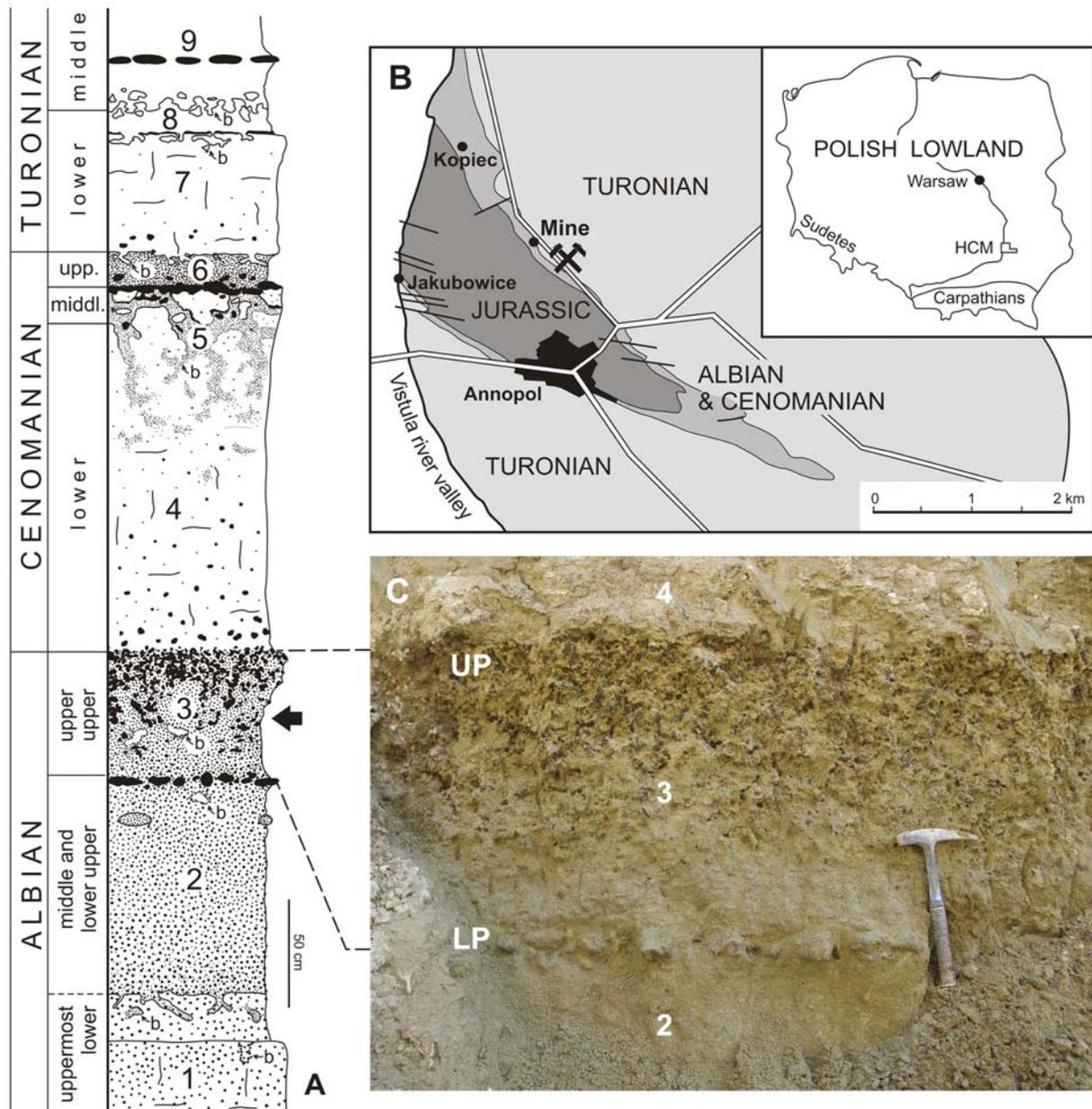
Unit 3 is ca. 50 cm thick and is composed of quartz sand with abundant glauconite, passing gradually upwards into quartzose-glauconitic marl. A distinct bed of phosphatic clasts, nodules and fossils occurs in the upper part of this unit. Its upper boundary is usually sharp, whereas the lower one is diffuse due to intensive mottling of the sediment by burrowing animals (Marcinowski and Walaszczyk 1985; Walaszczyk 1987). The phosphatic clasts are usually c. 1 cm in diameter, but in the upper part of the layer they are commonly cemented together, forming larger aggregates, up to 10–12 cm in diameter. These concretionary aggregates, composed of up to three generations of clasts, testify to a multi-phase origin and redeposition of the phosphate material (Marcinowski and Radwański 1983; Walaszczyk 1984).

The fossil assemblage from unit 3 is dominated by phosphatised lithistid sponges (including *Siphonia* sp.), calcitic-shelled bivalves, mainly *Aucellina gryphaeoides* and *Pycnodonte vesiculosa*, and guards of a small belemnite *Neohoplites ultimus*. Shells of rhynchonellid and terebratulid brachiopods, serpulid tubes and rare shrimp remains are subsidiary components of the invertebrate assemblage. Invertebrates are associated with relatively common vertebrate remains, including those of sharks, chimaeroid and bony fish, ichthyosaurs, plesiosaurs, marine turtles and occasional pterosaurs. The most numerous and best preserved fossils occur in the lower and middle part of the unit, those from its upper portion are commonly poorly preserved and overgrown by phosphates (see Text-fig. 1A, C).

OYSTER-BIOIMMURED AMMONITES FROM THE UPPER ALBIAN OF POLAND

Many oysters, aucellinas and brachiopods occur as phosphatic internal moulds lacking their original calcitic shells, possibly due to mechanical damage during reworking. No remains of originally aragonitic mollusks were recorded from unit 3 during the present study, except for the ammonite replicas preserved on oyster shells

described below. Many oysters are covered by phosphate overgrowths, which are occasionally present also in the attachment scars on their shells. In contrast, rare small specimens of a pycnodont oyster *Pycnodonte* sp. aff. *vesicularis* were found attached to phosphatic clasts near the top of unit 3.



Text-fig. 1. **A** – Lithology and stratigraphy of the condensed mid-Cretaceous succession of the Annapol anticline (modified after Walaszczuk, 1984). Units 1–9 are the transgressive-regressive units. 1. Quartzose sandstone, replaced upwards by quartz sands truncated by a burrowed surface. 2. Quartz sands with glauconite and rare sandstone nodules near the top; unit 2 is capped by a phosphate horizon. 3. Quartz sands with glauconite passing upwards into marly sands with glauconite and phosphates, forming a distinct horizon at the top of the unit. 4. Quartzose marls with glauconite and phosphates in the lower part. 5. Glauconitic marls infilling burrows in the underlying unit, truncated by a hardground with phosphate and glauconite impregnation. 6. Strongly glauconitic marls with burrowed omission surface at the top. 7. Limestone with rare phosphatic nodules and glauconite, capped by a hardground with glauconitic mineralisation. 8. Marls with burrowed omission surface at the top. 9. Marls with black flint; b – burrows. **B** – Geologic sketch-map of the Annapol anticline (modified after Walaszczuk, 1987) with localities studied (see text for further explanations) and location of the study area within Poland. **C** – Close-up view of the upper Upper Albian unit 3 at Kopiec. LP – lower part of the Phosphorite Bed, UP – upper part of the Phosphorite Bed. Arrowed is the middle portion of unit 3 which yielded the oyster-bioimmured ammonites studied

Substage	Ammonite Zones	Ammonite Subzones
LOWER CENOMANIAN (lower part)	<i>Mantelliceras mantelli</i>	<i>Mantelliceras saxbii</i> <i>Sharpeiceras schlueteri</i> <i>Neostlingoceras carcitanense</i>
UPPER ALBIAN	<i>Praeschloenbachia briacensis</i>	
	<i>Mortoniceras perinflatum</i>	
	<i>Mortoniceras rostratum</i>	
	<i>Mortoniceras fallax</i>	
	<i>Mortoniceras inflatum</i>	
	<i>Mortoniceras pricei</i>	
	<i>Diploceras cristatum</i>	
MIDDLE ALBIAN	<i>Euhoplites lautus</i>	<i>Anahoplites daviesi</i> <i>Euhoplites nitidus</i>
	<i>Euhoplites loricatus</i>	<i>Euhoplites meandrinus</i> <i>Mojsisovicsia subdelaruei</i> <i>Dimorphoplites niobe</i> <i>Anahoplites intermedius</i>
	<i>Hoplites dentatus</i>	<i>Hoplites spathi</i> <i>Lyelliceras lyelli</i>
LOWER ALBIAN (upper part)	<i>Otohoplites auritiformis</i>	<i>Lyelliceras pseudolyelli</i> <i>Pseudosonneratia steinmanni</i> <i>Otohoplites bulliensis</i> <i>Protohoplites puzosianus</i> <i>Otohoplites raulinianus</i>

Table 1. Biostratigraphic subdivision of the Albian and Lower Cenomanian in the Boreal Realm. The Lower and Middle Albian subdivision is based on Owen (1988, 2007, 2012); that for the Upper Albian on Kennedy and Latil (2007); the Lower Cenomanian subdivision and placement of the Albian–Cenomanian boundary is based on Kennedy *et al.* (2004) and Gale *et al.* (1996)

LOCALITIES, MATERIAL AND METHODS

Five specimens of oyster-bioimmured ammonites are recognised in the Upper Albian deposits of the Annopol anticline. These fossils were collected at the locality Kopiec, situated on the northern limb of the Annopol anticline, south of the village Kopiec (Text-fig. 1B). This is an old disused sandstone quarry and the fossils were collected here by means of screen-washing of sediment from a series of temporary trenches close to the quarry. Specimens from Kopiec and their silicone squeezes are housed in the Institute of Paleobiology, Polish Academy of Sciences (abbreviated ZPAL Am. 23/1-5).

In addition, a phosphatic mould of “*Stoliczkaia cf. notha*” of Cieśliński (1959) was examined. This specimen is housed in the Geological Museum of the Polish Geological Institute, National Research Institute (abbreviated MUZ PIG 955.II.77). It comes from a section near the village of Jakubowice on the Vistula river bank on the southern limb of the Annopol anticline (Text-fig. 1B), which is no longer accessible.

BIOIMMURING OYSTERS

Several oyster taxa have been identified from unit 3 of the Annopol succession, based on records from surface outcrops and the underground phosphorite mine (see Text-fig. 1B). These are: very rare *Rastellum diluvianum* (subfamily Paleolophinae), rare “*Exogyra*” sp. and *Gryphaeostrea canaliculata* (subfamily Exogyriinae), very common *Pycnodonte vesiculosa*, and rare *Pycnodonte* sp. aff. *vesicularis* (subfamily Pycnodontinae), and a single individual of ?*Agerostrea* sp (subfamily Liostreinae) (suprageneric oyster taxonomy follows that of Malchus 1990).

The most common oyster in unit 3 is *Pycnodonte vesiculosa*, which occurs here in hundreds of individuals. This is a relatively small oyster which preferred to lift its commissure off the substrate at the very early growth stages, like many other oysters adapted to live on soft muddy bottoms (e.g., Stenzel 1971; Machalski 1998). This resulted in a gryphaeate shape of the shell and in a small attachment scar, not suitable for identification of the

substrate (see also Woods 1913; Seeling and Bengtson 1999; Wilmsen and Voigt 2006). In contrast, forms identified here as *Pycnodonte* sp. aff. *vesicularis* are larger. Their growth strategy was to follow the substrate as long as possible, which resulted in relatively large attachment surfaces, preserving details of the substrate.

The oyster-bioimmured ammonites were recognised on the left valves of five exogyrine and pycnodonteine individuals coming from the middle portion of unit 3 (Text-fig. 1A, C). These are “*Exogyra*” sp. (ZPAL Am. 23/3, Text-fig. 2E, F), *Gryphaeostrea canaliculata* (ZPAL Am. 23/4, Text-fig. 2 C, D), and *Pycnodonte* sp. aff. *vesicularis* (ZPAL Am. 23/1, 2, 5, Text-figs 2A, B, G, H, 4C).

BIOIMMURED AMMONITES AND BIOSTRATIGRAPHY

The present material consists of five ammonite replicas preserved as attachment scars on oyster left valves (Text-figs 2A, C, E, G, 4C). Silicone squeezes of four specimens illustrated in Text-fig. 2 are shown in Text-fig. 3A, C–E. Taken together, these specimens can be referred to the genus *Mortoniceras* Meek, 1876, an exclusively Upper Albian genus. More refined dating depends on determination of the subgenus present.

Specimen ZPAL Am. 23/1 (Text-figs 2A, 3A) is the mould of an umbilicus just over 16 mm in diameter. Ten to eleven ribs per half whorl arise at the umbilical seam, strengthen across the umbilical wall and shoulder and develop into an umbilicolateral bulla, from which a blunt, rounded, prorsiradiate rib develops, with a pair of ribs arising from a bulla towards the adapertural end of the mould. There are no indications of other tubercles at the smallest preserved diameter, but at the largest preserved diameter there is a suggestion of a lateral bulla.

Specimen ZPAL Am. 23/2 (Text-figs 2G, 3C) is the mould of an umbilicus with an estimated umbilical diameter of 26 mm. Most of the ribs are single primaries, as in the previous specimen, with a pair of ribs arising from an umbilical bulla towards the adapertural end of the mould. The same pattern of predominantly single primaries is seen in specimen ZPAL Am. 23/4 (Text-figs 2C, 3D), part of the umbilical shoulder and inner flank, with well-preserved umbilical and lateral bullae.

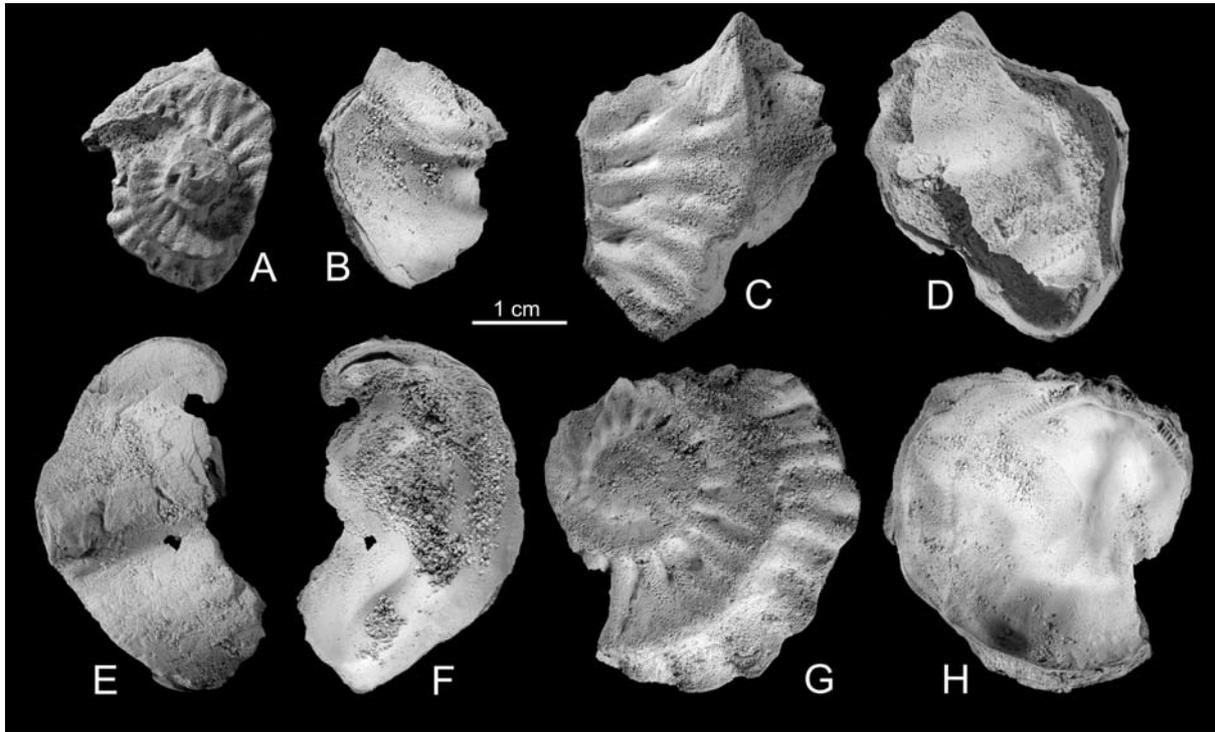
Specimen ZPAL Am. 23/3 (Text-figs 2E, 3E) preserves part only of three ribs, and appears to be from either the umbilical or ventrolateral region, and does not contribute to the precise identification of the taxon involved.

The key features of the present material are the crowded, predominantly single ribs with occasional pairs

of ribs arising from umbilical bullae, and the presence of a lateral bulla from an early (but not the earliest) growth stage. The presence of the lateral bulla from an early stage suggests the subgenus *Subschloenbachia* Spath, 1921 (= *Durnovarites* Spath, 1932; *Reyericeras* Collignon, 1979; see discussion in Kennedy *et al.* 1988) and thus the *Mortoniceras rostratum* or *M. perinflatum* Zone of the upper Upper Albian zonal sequence proposed by Kennedy and Latil (2007) (see Table 1). The closest comparison is with *Mortoniceras perinflatum* Zone forms, where the lateral bulla is present at a very early stage, as in the holotype of *Mortoniceras (Subschloenbachia) postinflatum* Spath, 1933, illustrated here as Text-fig 3B.

The fifth individual studied (ZPAL Am. 23/5, see Text-fig. 4C) clearly belongs to another ammonite taxon and is possibly a phragmocone fragment. The specimen seems to have either bifurcating, or alternate primary and secondary ribs that broaden across the flanks and flex back and are rursiradiate on the outer flank. This indicates a specifically indeterminate *Stoliczkaia*, comparable to *Stoliczkaia (Stoliczkaia) flexicostata* Breistoffer, 1940, as described by Renz (1968, p. 49, pl. 6, fig. 9) and *Stoliczkaia notha inflata* Spath, 1931, as described by by the same author (Renz 1968, p. 50, pl. 6, fig. 8).

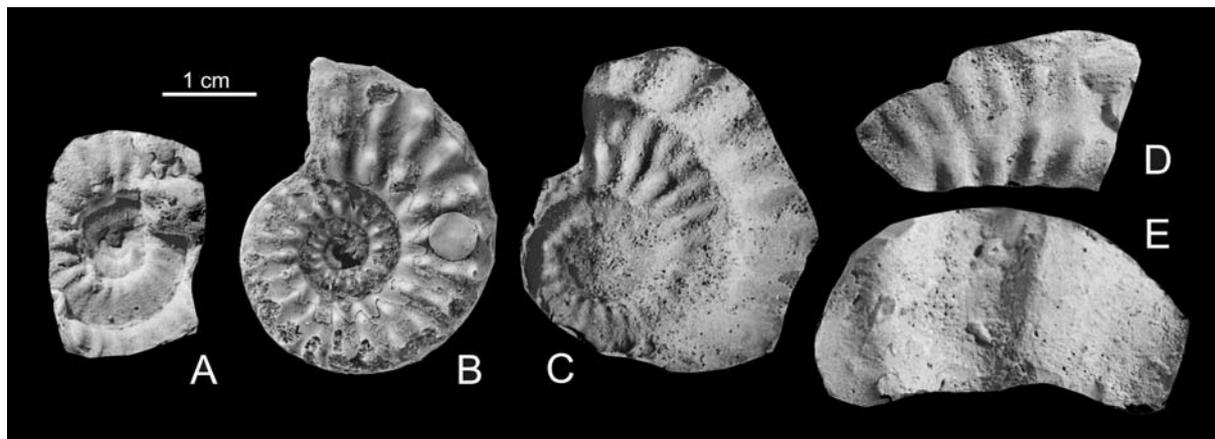
It should be noted here that the only ammonite specimen known from unit 2 prior to the present study is a specimen referred to as *Stoliczkaia cf. notha* by Cieśliński (1959). It comes from the upper part of the Phosphorite Bed as exposed at Jakubowice. The specimen was briefly described by Cieśliński (1959, p. 66), but was never illustrated. It is figured herein (Text-fig. 4A, B). The specimen is a fragment of body chamber with coarse ribs, and clearly belongs to *Stoliczkaia*, but is specifically and subgenerically indeterminate. Coarse ribbing of this type is seen in *Stoliczkaia (Stoliczkaia) notha* (Seeley, 1865) as with examples figured by Spath (1931, pl. 31, figs 1, 5, 6), Wright and Kennedy (1994, fig. 10c–j), and Kennedy and Delamette (1994, figs 10.19–10.21), where it can be concave across the venter. The ventral ribbing of some Cenomanian *Stoliczkaia (Lamnayella)* is also comparable, as with *S. (L.) sanctaecatherinae* Wright and Kennedy, 1978, figured by Kennedy and Delamette (1994, figs 10. 9, 10, 15). Some specimens referred to *S. notha* are much finer ribbed than present fragment at the same size (Spath 1931, pl. 31, fig. 8). The very coarse ribbing of *S. notha* appears to be an adult body chamber character. The specimen might be a fragment of a microconch body chamber of *S. notha* and compared to the small adult figured by Spath (1931, pl. 31, fig. 6: his variety *inflata*; see also Wright and Kennedy 1994, fig. 10c, d), but there is just not enough of it for confident



Text-fig. 2. Bioimmuring oysters with attachment scars preserving replicas of *Mortoniceras* (*Subschloenbachia*) sp., middle portion of unit 3 (upper part of the Phosphorite Bed), upper Upper Albian, locality Kopiec, Annapol. A, B, G, H – *Pycnodonte* sp. aff. *vesicularis* (A, B, ZPAL Am. 23/1, G, H, ZPAL Am. 23/2). C, D – *Gryphaeostrea canaliculata*, ZPAL Am. 23/4. E, F. “*Exogyra*” sp., ZPAL Am. 23/3. A, C, E, G are external views of the left valves; F, H are internal views of the left valves; B, D are external views of the right valves

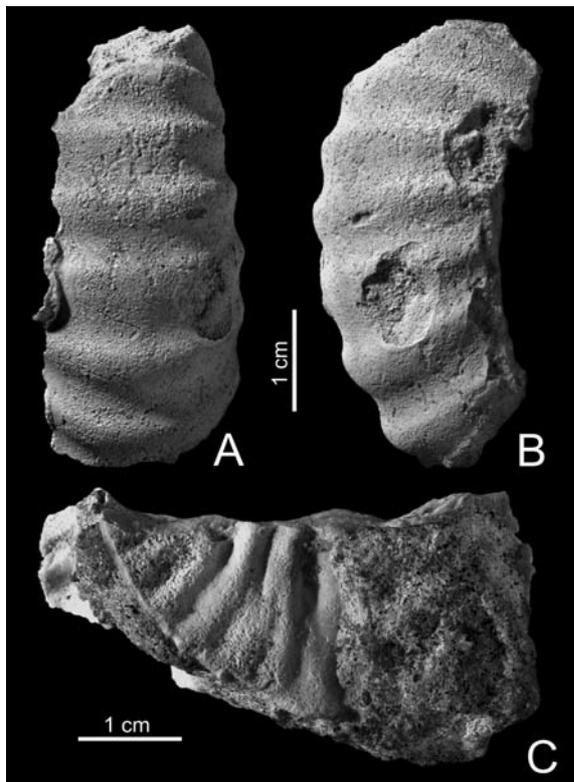
determination. The specimen has an appearance of an internal mould. However, in view of the absence of this preservation in the level it comes from, it is possible that it represents a phosphorite cast of an ammonite replica originally preserved as an attachment scar on oyster shell, which was lost.

In summary, the ammonites from unit 3 indicate *Mortoniceras rostratum* or, more probably, the *M. perinflatum* Zone of the upper Upper Albian zonal sequence proposed by Kennedy and Latil (2007) (see Table 1), thus a level within the classic but now abandoned upper Upper Albian *Stoliczkaia dispar* Zone of authors. Ironically,



Text-fig. 3A, C-E – Silicone squeezes of the oyster-preserved replicas of *Mortoniceras* (*Subschloenbachia*) sp. from the middle portion of unit 3 (upper part of the Phosphorite Bed), upper Upper Albian, locality Kopiec, Annapol. A – ZPAL Am. 23/1, C – ZPAL Am. 23/2, D – ZPAL Am. 23/4, E – ZPAL Am. 23/3. B – the holotype of *Mortoniceras* (*Subschloenbachia*) *postinflatum* Spath, 1933, pl. 40, fig. 5, no. C55362 in the collections of the Natural History Museum, London, from the *Mortoniceras perinflatum* Zone ammonite bed in the Upper Greensand at Holworth House, east of Weymouth, Dorset (photo supplied by the Photographic Unit of the Natural History Museum, London)

OYSTER-BIOIMMURED AMMONITES FROM THE UPPER ALBIAN OF POLAND



Text-fig. 4. A-C – *Stoliczkaia* sp. from unit 3 (upper part of the Phosphorite Bed), upper Upper Albian, Annopol. A, B – Phosphorite mould of “*Stoliczkaia* cf. *notha*” of Cieśliński (1959), part of the body chamber, MUZ PIG 955.II.77 from Jakubowice (A, ventral, B, lateral views). C – oyster-bioimmured specimen, part of the phragmocone, from Kopiec (ZPAL Am. 23/5)

this latter assignment is in agreement with those of earlier authors (e.g., Marcinowski and Wiedmann 1985, 1990), although their conclusions were based on the specimen of *Stoliczkaia* cf. *notha* reported by Cieśliński (1959), which is regarded here as specifically undeterminable.

THE ALBIAN–CENOMANIAN BOUNDARY HIATUS

In many parts of Europe, the Albian–Cenomanian (Lower/Upper Cretaceous) boundary is marked by a distinct lithological change at a strongly burrowed erosion surface (Gale *et al.* 1996; Robaszynski *et al.* 1998; Wilmsen 2003). The underlying Albian is represented by a variety of facies, including greensands. The Lower Cenomanian sediments are usually developed as strongly bioturbated calcareous glauconitic sands as exemplified by the Glauconitic Marl of SE England, the Tourtia in NE France and Belgium, and the Essen Greensand Formation in northern Germany. There is a gap at the Albian–Cenomanian boundary in

these sections and its extent can be evaluated by comparison with the expanded basal sections, like that exposed at Mont Risou near Rosans (Hautes Alpes) which is the Global Reference Section and Point (GSSP) for this boundary (Gale *et al.* 1996; Kennedy *et al.* 2004).

At Annopol, the contact between the Albian phosphorites (top of unit 3) and the Cenomanian marls (unit 4) is also abrupt (Text-fig. 1A, C). This is the Discontinuity No. 2 distinguished by Walaszczyk (1987). This sedimentary discontinuity was recognised for the first time by Cieśliński (1976), who postulated a stratigraphic gap at this level, corresponding to the Lower and ?low-Middle Cenomanian. Marcinowski (1980) rejected this view, based on the occurrence of ammonite indices for all the Lower Cenomanian ammonite zones and subzones in the overlying Cenomanian marls.

The oyster-bioimmured ammonites place unit 3 of the Annopol succession in the *Mortoniceras rostratum* or *Mortoniceras perinflatum* Zone of the upper Upper Albian (see Table 1), with stronger indication for the latter zone (see above). No ammonites indicative of the uppermost Albian–lowermost Cenomanian *Praeschloenbachia briacensis* Zone are recorded. Thus, the hiatus at the Albian–Cenomanian boundary at Annopol embraces this zone, a situation analogous to many condensed sections of the Boreal Realm (e.g., in the Anglo-Paris Basin, see Gale *et al.* 1996 and Amédro 2002).

The upper range of the Albian–Cenomanian hiatus in the Annopol succession cannot be precisely determined in view of the fact that ammonite specimens preserved in the lower part of the Cenomanian marls (lower part of the unit 4 in Text-fig. 1A) are represented exclusively by phosphorite moulds (Walaszczyk 1984). Fossils of this state of preservation may, or may not be, of the same biostratigraphic position as their surrounding matrix. Moreover, it is not known whether these specimens occurred in a stratigraphic succession or represent a totally mixed fossil assemblage as originally proposed by Marcinowski (1980).

PALAEOBIOGEOGRAPHIC IMPLICATIONS

The genus *Mortoniceras*, recognised herein on the basis of the oyster-bioimmured specimens from the upper Upper Albian of the Annopol area, belongs to Brancoceratidae, which is a typically Tethyan ammonite family (e.g., Marcinowski and Wiedmann 1985). The representatives of this genus are relatively

common in the ammonite assemblage recorded from the lower Upper Albian sands of the Mt. Chełmowa section by Marcinowski and Wiedmann (1985, 1990). In contrast, only a single specimen of *Mortoniceras* was reported by these authors from the Annopol succession. This was an individual of *Mortoniceras* cf. *inflatum* from the lag of the reworked phosphatic concretions and clasts forming the top of unit 2 (Text-fig. 1A, C).

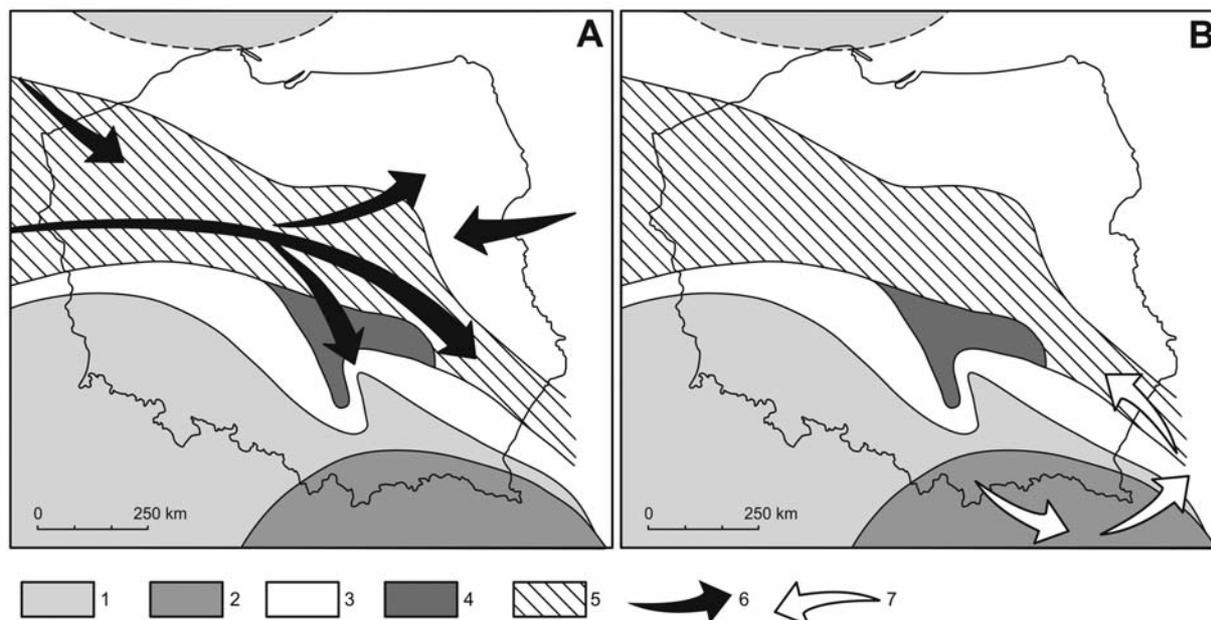
According to Marcinowski and Wiedmann, the scarce representation of *Mortoniceras* in Annopol and its common occurrence in the more westerly Mt. Chełmowa section “excluded the possibility of its migration from the Carpathian geosyncline through the Lwów region” (Marcinowski and Wiedmann 1985, p. 213–214; see Text-fig. 5A for their vision of the ammonite migration routes in Late Albian of Poland and adjacent areas). These authors suggested that Brancoceratidae migrated from “the Alpine geosyncline to the Central European Basin via the London-Paris Basin” (Marcinowski and Wiedmann 1985, p. 214). The present records of the oyster-bioimmured *Mortoniceras* individuals from the top of the Albian succession at Annopol put this conclusion in doubt.

There are four *Mortoniceras* and two *Stoliczkaia* individuals in the studied material. Assuming that the oysters did not prefer the shells of *Mortoniceras* as settling substrates, one may conclude that the numerical ratio between *Mortoniceras* and *Stoliczkaia* reflects

that in the original ammonite assemblage. This suggests that the representatives of *Mortoniceras* were the commonest ammonites in the Annopol area during the late Late Albian. This indicates, in turn, that the Annopol site does not mark any gap in the geographic distribution of *Mortoniceras* in Poland. Consequently, the representatives of this genus could migrate into the epicratonic areas of Poland directly from the Tethyan Realm, via the Lwów area (see Text-fig. 5B).

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Text-fig. 5. A, B – Late Albian palaeogeography of Poland and adjacent areas (modified after Marcinowski and Wiedmann 1985, fig. 1C) with the hoplitid migration routes proposed by Marcinowski and Wiedmann 1985 for the early Late Albian (A) and a possible migration route of *Mortoniceras* in the late Late Albian as suggested in the present paper (B). 1 – land areas, 2 – flysh; 3 – sands; 4 – gaizes and spongiolites; 5 – sandy marls and marly sands; 6 – routes of hoplitid migration; 7 – routes of *Mortoniceras* migration

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