

Original Article

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The brachiopod assemblage from the Maastrichtian white chalk at Chełm, eastern Poland: stratigraphical and palaeoecological implications

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Abstract

Brachiopods from the lower upper Maastrichtian (Upper Cretaceous) white chalk succession exposed at Chełm (eastern Poland) comprise *Lingula cretacea*, *Isocrania costata*, *Cryptoporella antiqua*, *Cretirhynchia* sp., *Neoliothyris* sp., *Carneithyris* sp., *Terebratulina chrysalis*, *T. faujasi*, *T. longicollis*, *Terebratulina* spp., *Gisilina* sp., *Bronnothyris bronni*, *Magas chitoniformis*, *Leptothyrellopsis polonicus* and ?*Aemula* sp. This assemblage is relatively poor in terms of taxonomic diversity and specimen abundance and is dominated by stratigraphically long-ranging species. It is best comparable to that from the micromorphic brachiopod *Rugia tenuicostata*–*Meonia semiglobularis* Zone as distinguished in the white chalk successions of Denmark and northern Germany, although this zone is usually placed in the upper lower Maastrichtian. The Chełm succession represents a relatively deep-water and ‘benthos-poor’ variety of white chalk deposited in the Boreal Chalk Sea of Europe. The brachiopod assemblage studied is typical of such a habitat, having been controlled largely by the low availability of minute skeletal substrates suitable for brachiopod settlement.

Introduction

Brachiopods are an important component of white chalk macrofossil assemblages that thrived in the Boreal Chalk Sea of Europe during the Campanian and Maastrichtian (Late Cretaceous). They have been widely used for stratigraphical and palaeoecological inferences (e.g., Steinich, 1965; Surlyk, 1970, 1972, 1982; Bitner & Pisera, 1979; Ernst, 1984; Johansen, 1987a, b; Johansen & Surlyk, 1990; MacKinnon et al., 1998; Jelby et al., 2014; Schröder & Surlyk, 2020). As far as stratigraphy is concerned, Surlyk (1972, 1984) proposed a biostratigraphical scheme for the upper Campanian and Maastrichtian in northwest Europe, comprising several zones based on micromorphic brachiopod assemblages recovered mainly from sections in Denmark (several localities in Jylland and Sjælland; Johansen, 1987a) and northwest (Kronsmoor and Hemmoor sections, Surlyk, 1982; Johansen, 1987b) and northeast Germany (Isle of Rügen, Steinich, 1965).

In Poland, brachiopods from the Upper Cretaceous white chalk facies have been described to date only from the Campanian succession at Mielnik on the River Bug (Bitner & Pisera, 1979; see Bojanowski et al., 2017 for an updated stratigraphy). The aim of the present paper is to describe, for the first time, a brachiopod assemblage from the lower upper Maastrichtian chalk at Chełm, eastern Poland (Fig. 1A, B), and to discuss its stratigraphical and palaeoecological significance within the context of previous work on Late Cretaceous brachiopod assemblages from the European white chalk.

Geological setting

The studied brachiopod-bearing chalk succession crops out in an active chalk quarry run by the cement company Cemex Polska (Fig. 1B), situated in the eastern part of the town of Chełm. Currently, the chalk is accessible along four exploitation levels that are referred to, from the top to the bottom, as II, III, IV and V. Level I has now been completely excavated. A portion of the section below level V temporarily exposed in a dewatering trench was referred to as level VI by Dubicka & Peryt (2011). The total thickness of the chalk currently exposed at Chełm is c. 40 m, with the top of working level II located at 203 m a.s.l. (above sea level), and the bottom of level VI at 164 m a.s.l. (Dubicka & Peryt, 2011; Machalski et al., 2021).

The white chalk exposed at Chełm (Fig. 2) is a fine-grained carbonate deposit composed almost exclusively of coccoliths. Flint layers, burrowed omission surfaces, bored and/or mineralised hardgrounds and other marker beds, which are characteristic of many white chalk successions in Europe, are absent. The only indication that the chalk strata at Chełm lie almost horizontally is

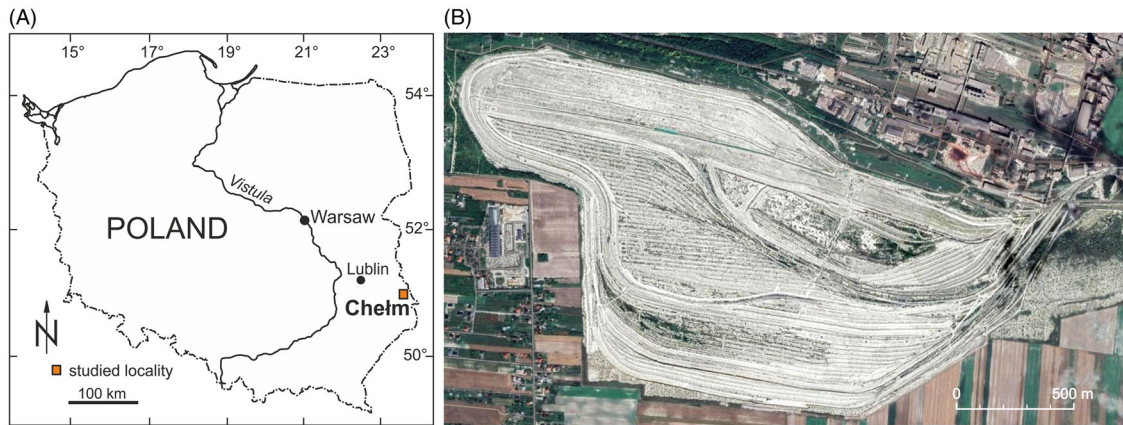


Figure 1. A. Location of the Chelm site in Poland (modified from Machalski et al., 2021, Fig. 1). B. Satellite view of the Chelm chalk pit (Google Maps, <https://www.google.com/maps/place/Chelm>).

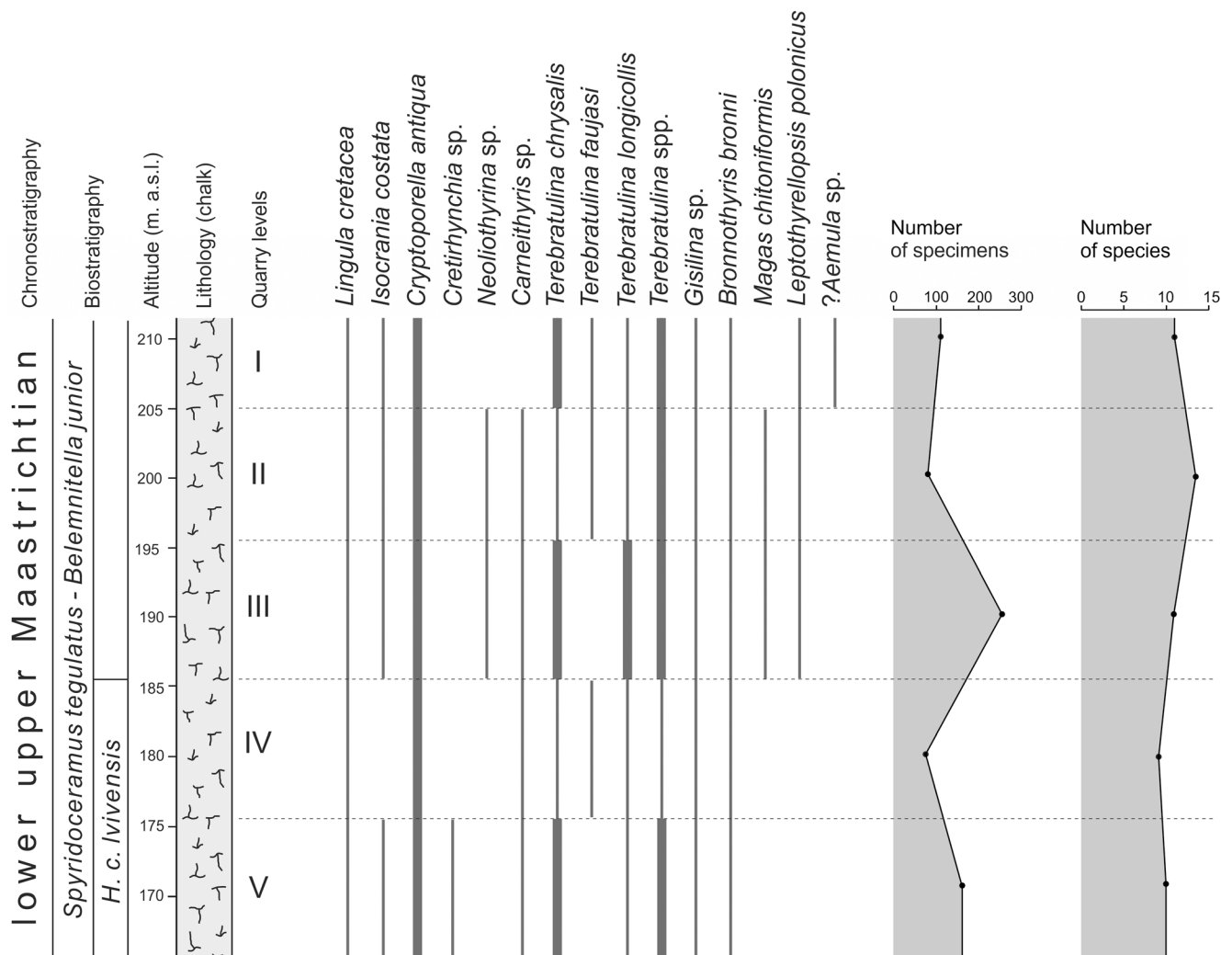


Figure 2. Distribution of brachiopod species recognised in the lower upper Maastrichtian section exposed at Chelm along the section log and macrofossil biostratigraphy; vertical bars mark the occurrence of identified brachiopod taxa: thick – common, thin – rare (see text for further details).

provided by the orientation of some fossils, for instance, tests of irregular echinoids (*Echinocorys* sp.) preserved in life position (Dubicka & Peryt, 2011). In view of this, the exploration levels are

the only reference for sampling (Dubicka & Peryt, 2011; Machalski et al., 2021). See the ‘Supplementary Information’ in Machalski et al. (2021) for a full description of the section and its fossil assemblages.

Macrofossil assemblages at Chełm are rather poor in diversity and number of specimens, being dominated by small- to medium-sized bivalves, echinoids and ammonites (Dubicka & Peryt, 2011; Machalski et al., 2021). In terms of macrofossil biostratigraphy (Fig. 2), the chalk succession at Chełm has been assigned by Machalski (2005) and Dubicka & Peryt (2011) to the lower upper Maastrichtian *Belemnitella junior* Zone and the *Spyridoceramus tegulatus*–*Belemnitella junior* Zone in the conventional subdivisions of the Boreal Maastrichtian in Europe (see, e.g., Błaszkiwicz, 1980; Schulz & Schmid, 1983; Christensen et al., 2005). According to Walaszczyk et al. (2016), the Chełm succession represented the uppermost ‘true’ (non-*tegulatus*) inoceramid ‘*Inoceramus*’ *ianjonaensis* Zone also put in the lower upper Maastrichtian, as based on data from the Vijlen Member in northeast Belgium and the Aachen area in western Germany (see Walaszczyk et al., 2010). It is worth mentioning in this context that no ‘true’ inoceramids are known to date from Chełm, *Spyridoceramus tegulatus* (von Hagenow, 1842) being the sole representative of the ‘*tegulatus* inoceramids’ throughout the section. Belemnites at Chełm are represented by very rare individuals of *Belemnitella junior* Nowak, 1913 and *B. lwowensis* Naidin, 1952 (see Dubicka & Peryt, 2011). Both species are present in the lower part of the upper Maastrichtian of the Hemmoor section, northwest Germany and in the Haccourt-Lixhe area of northeast Belgium (Christensen et al., 2005). In ammonite terms, levels V and IV belong to the lower upper Maastrichtian scaphitid ammonite *Hoploscaphites constrictus livivensis* Zone (Machalski et al., 2021; Fig. 2 herein).

Dubicka & Peryt (2012) assigned the Chełm section to their local foraminiferal zones VIII (lowest part), IX (bulk of section) and X (top of section). Based on planktic foraminiferal spectra (Dubicka & Peryt, 2011, 2012) and the shape of the carbon isotope curve, Machalski et al. (2021; Supplementary Information) concluded that the Chełm section corresponded to the interval between *c.* 180 and 115 m in the Stevns-1 reference borehole in Denmark, as described by Thibault et al. (2012) and Surlyk et al. (2013). This interval represents the Hvidskud Member of the Møns Klint Formation, which comprises the topmost part of the UC19, entire UC20a and lower part of the UC20b-c nannofossil zones, and three magnetostratigraphic zones, namely 31n, 30r and 30n. This corresponds to the topmost part of the lower Maastrichtian (level VI not studied for brachiopods for the present paper) and the lower part of the upper Maastrichtian (remaining levels, see Supplementary Information figure 2 in Machalski et al., 2021).

The Chełm chalk was deposited in an epicontinental setting, in the eastern part of the Boreal Chalk Sea of Europe (e.g., Surlyk et al., 2003; Engelke et al., 2016, 2017). The Chełm chalk matches the characteristics of the ‘benthos-poor’ variety of white chalk in the Boreal Chalk Sea facies model, representing the deepest epicontinental chalk facies, deposited below the photic zone and storm wave base (Surlyk et al., 2003, Fig. 13.7; see also Surlyk & Birkelund, 1977 and Hansen & Surlyk, 2014). Similar to other examples of this white chalk subfacies, the Chełm chalk is monotonous and lacks hardgrounds, omission surfaces, scour horizons, tabular fossil concentrations and flint nodules. Its macrofossil content is typified by a rather poor macrobenthic assemblage, a predominance of *Zoophycos* burrows (at least in the lower levels), a relative abundance of ammonites and an extreme rarity of belemnites represented solely by adult individuals (Machalski et al., 2021). A shallowing-upwards trend is inferred from planktic foraminiferal data for the succession (Dubicka & Peryt, 2011, 2012), with depth estimates ranging from >100 m for the lower levels to several dozen metres in the uppermost part of

the section (Machalski et al., 2021). Correlation with the planktic foraminiferal spectra recorded from equivalent Maastrichtian levels in the Middle Vistula River section (central Poland) suggests that the record of the maximum mid-Maastrichtian sea level rise should be expected just beneath the bottom of the section exposed at Chełm (Dubicka & Peryt, 2011, 2012).

Material and methods

The brachiopod samples studied herein were collected in the late 1980s, at a time when level I of the Chełm quarry was still in existence, but level VI had yet to be developed. Therefore, these samples originate from levels I to V (Fig. 2).

The brachiopod assemblage studied, 729 specimens in all, comprise both macro- and micromorphic brachiopods. All micromorphic brachiopods studied herein come from bulk samples from levels I to V. Each of these samples weighed between 8 and 12 kg, yielding 109 specimens from level I, 94 from II, 267 from III, 87 from IV and 172 from V. After boiling in a Glauber-Salt solution, the samples were washed and wet-sieved at mesh widths of 0.5 mm at the laboratory. Only few macrobrachiopods were collected directly in the field by handpicking from chalk surfaces. The frequency of brachiopods at each level is low, and their preservation is relatively poor – many individuals are damaged or crushed and there are also many fragments in washing residues. It is impossible to assess whether the fragmentation resulted from sample processing or from original fossil preservation. Considering this and the fact that the precise weight of each sample was not recorded before preparation, the brachiopod frequency is given only in qualitative terms (i.e., rare vs common where a number of up to 25 specimens per level is considered as rare) in the present paper (Fig. 2). In addition to brachiopods, the washing residues from Chełm yielded a rather meagre lot of organic remains composed of fragments of calcitic bivalve shells, cirripede plates, echinoderm remains (crinoid columnals and echinoid spines) and rare bryozoan fragments.

Specimens selected for scanning electron microscopy were mounted on stubs, coated with platinum and photographed using a Philips XL-20 microscope at the Institute of Paleobiology, Warszawa. The material is housed at the Institute of Paleobiology under the collection number ZPAL Bp.50.

Taxonomy

In total, 15 brachiopod taxa have been recovered from the chalk succession at Chełm (Table 1). These are *Lingula cretacea* Lundgren, 1885, *Isocrania costata* (Sowerby, 1823) (Fig. 3G–I), *Cryptoporella antiqua* Bitner & Pisera, 1979 (Fig. 4A–H), *Cretirhynchia* sp., *Neoliothyryna* sp., *Carneithyris* sp., *Terebratulina chrysalis* (Schlotheim, 1813) (Fig. 3C), *T. faujasi* (Roemer, 1841), *T. longicollis* Steinich, 1965 (Fig. 3A, B), *Terebratulina* spp., *Gisilina* sp., *Bronnothyris bronni* (Roemer, 1841) (Fig. 3E, F), *Magas chitoniformis* (Schlotheim, 1813) (Fig. 3D), *Leptothyrellopsis polonicus* Bitner & Pisera, 1979 and ?*Aemula* sp. (Fig. 2; Table 1). Only *Cryptoporella antiqua* and some species of *Terebratulina* are common in the material studied, while others are rare (Fig. 2; Table 1). Six taxa were identified at all levels sampled for brachiopods (Fig. 2). Of these, the presence of *Lingula cretacea* is worth noting; this is represented by poorly preserved fragments throughout the section. Cretaceous to Recent representatives of *Lingula* have been characterised by a very low taphonomic potential in view of thin fragile shell, composed of

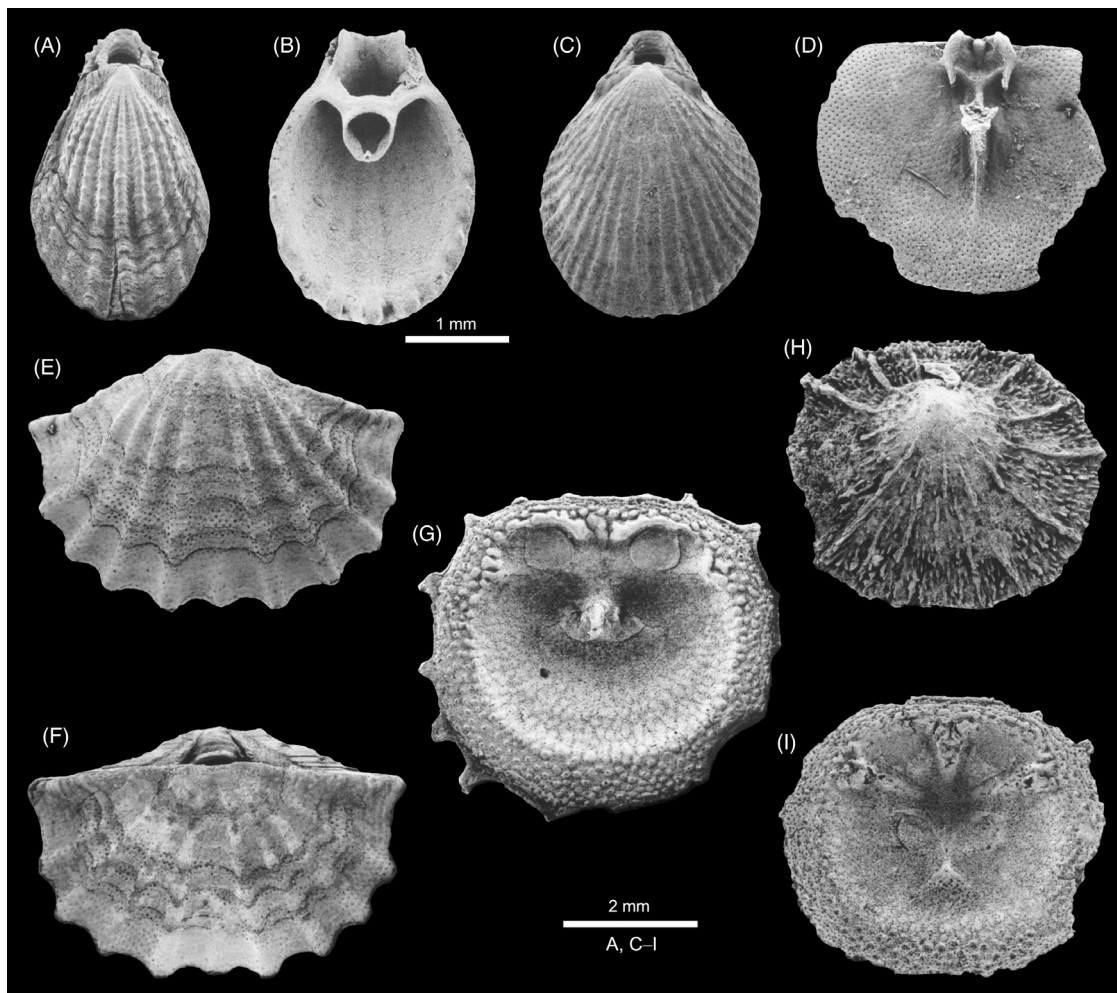


Figure 3. Selected brachiopods from the lower upper Maastrichtian white chalk exposed at Chelm. A, B. *Terebratulina longicollis*; A – dorsal view of complete specimen, level IV, ZPAL Bp.50/8; B – inner view of dorsal valve to show brachidium, level V, ZPAL Bp.50/9; C – *Terebratulina chrysalis*, dorsal view of complete young specimen, level III, ZPAL Bp.50/7; D – *Magas chitoniformis*, inner view of dorsal valve, level III, ZPAL Bp.50/10; E, F – *Bronnothyris bronni*, ventral and dorsal views of complete specimen, level II, ZPAL Bp.50/11; G–I – *Isocrania costata*; G – inner view of ventral valve, level II, ZPAL Bp.50/1; H, I – outer and inner views of dorsal valve, level II, ZPAL Bp.50/2. All SEM photomicrographs.

chitinous and phosphatic layers (Emig, 1990; Kowalewski & Flessa, 1996).

There is some variation in brachiopod diversity throughout the section, ranging from a minimum number of 9 taxa recorded from level IV to a maximum of 13 taxa from level II (Fig. 2). The number of specimens also varies between samples, ranging from a minimum number of 87 specimens in a sample from level IV to a maximum of 267 from level III (Fig. 2).

Most of the taxa identified at Chelm are common in the white chalk facies of northwest Europe, which are characterised by long stratigraphical ranges and a wide geographical distribution (compare Fig. 2 and Table 1 herein with Surlyk, 1984, Fig. 2; see also Surlyk, 1972). A notable exception is *Cryptoporella antiqua* (Fig. 4A–H), known so far only from the lower to upper Campanian of Mielnik (Bitner & Pisera, 1979; stratigraphy based on Bojanowski et al., 2017). Contrary to the Mielnik assemblage, this species dominates in the material from Chelm, constituting more than 40% of the material. Another species erected based on Mielnik material by Bitner & Pisera (1979) is *Leptothyrellops polonicus*. This was recovered by these authors from the chalk interval corresponding to the lower Campanian in currently accepted stratigraphy of the Mielnik section (Bojanowski et al.,

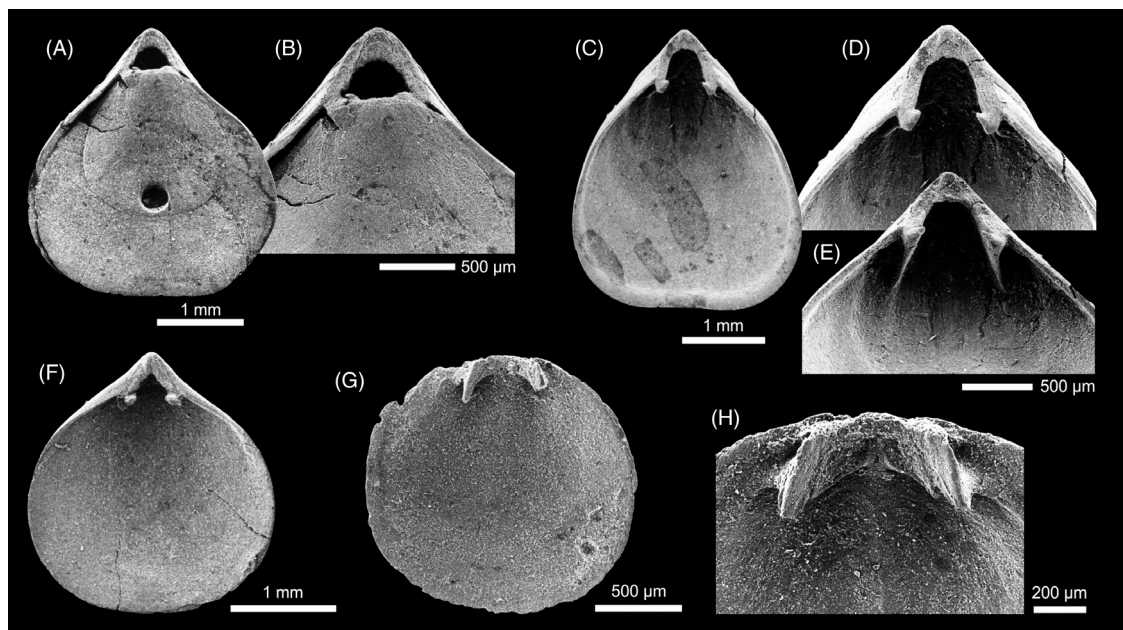
2017). This species has subsequently been recognised in the chalk facies of late Campanian and early Maastrichtian age in northern Europe (Surlyk, 1982; Johansen & Surlyk, 1990; MacKinnon et al., 1998; Simon & Mottequin, 2018).

With a total of 15 identified taxa, the Chelm assemblage is rather poor in comparison with the most prolific white chalk brachiopod assemblages, described from the lower lower and upper upper Maastrichtian of Denmark (Surlyk, 1972, Fig. 3; Surlyk, 1984, Fig. 1). For example, the assemblage from the *Argyrotheca stevensis*–*Magas chitoniformis* Zone at the top of the Danish Maastrichtian comprises 23 species, and those from the *Rugia spinosa*–*Terebratulina subtilis*, *T. subtilis*–*Trigonosemus pulchellus* and *T. pulchellus*–*T. pulchellus* zones from the middle portion of the lower Maastrichtian yield 22, 23 and 24 species, respectively. In contrast, the assemblage from the *Rugia tenuicostata*–*Meonia semiglobularis* Zone of Surlyk (1984) comprises 16 species, which is the minimum number for the Danish Maastrichtian, matching well the Chelm assemblage as far as taxonomic diversity is concerned.

In terms of number of individuals per standard 10 kg sample, the Danish chalk assemblages yield from over 3,000 specimens (*Argyrotheca stevensis*–*Magas chitoniformis* and *Terebratulina*

Table 1. Ecological groups of brachiopods identified from the lower upper Maastrichtian chalk exposed at Chelm and their relative abundance in the section (generalised, based on all levels). In parentheses, numbers of the groups after Schröder & Surlyk (2020) are shown.

Species	Ecological group	Abundance
<i>Lingula cretacea</i>	Burrowing, soft substrate (7)	Rare
<i>Isocrania costata</i>	Cemented, small attachment surface (6)	Rare
<i>Cryptoporella antiqua</i>	Attached with pedicle, small hard substrates (1)	Common
<i>Cretirhynchia</i> sp.	Secondarily free-living (4)	Rare
<i>Neoliothyris</i> sp.	Attached with pedicle, large hard substrates (2)	Rare
<i>Carneithyris</i> sp.	Secondarily free-living (4)	Rare
<i>Terebratulina chrysalis</i>	Attached with rootlet pedicle, soft substrate (3)	Common
<i>Terebratulina faujasi</i>	Attached with pedicle, small hard substrates (1)	Rare
<i>Terebratulina longicollis</i>	Attached with pedicle, small hard substrates (1)	Common
<i>Terebratulina</i> spp.	Attached with pedicle, small hard substrates (1)	Common
<i>Gisilina</i> sp.	Attached with pedicle, small hard substrates (1)	Rare
<i>Bronnothyris bronni</i>	Attached with pedicle, small hard substrates (1)	Rare
<i>Magas chitoniformis</i>	Secondarily free-living (4)	Rare
<i>Leptothyrelloopsis polonicus</i>	Attached with pedicle, small hard substrates (1)	Rare
? <i>Aemula</i> sp.	Attached with pedicle, small hard substrates (1)	Rare

**Figure 4.** *Cryptoporella antiqua* from the lower upper Maastrichtian white chalk exposed at Chelm, ZPAL Bp. 50/3-6. A, B – Dorsal view of complete specimen and enlargement of umbonal part to show details of beak, respectively. C–E – Inner view of ventral valve, enlargement of umbonal part and oblique view to show ventral plates, respectively. F – Inner view of ventral valve. G, H – Inner view of dorsal valve and enlargement of posterior part to show details of cardinalia, respectively. All SEM photomicrographs.

subtilis–*Trigonosemus pulchellus* zones) to several hundred specimens in the *Rugia tenuicostata*–*Meonia semiglobularis* Zone (Surlyk, 1972, Fig. 3). The specimen abundance at Chelm, ranging from 87 to 267 specimens per sample, is much lower than in any of the samples studied by Surlyk, including those from the *Rugia tenuicostata*–*Meonia semiglobularis* Zone, which are the poorest in specimens within the entire Danish Maastrichtian.

Stratigraphical position

As pointed out above, the Chelm assemblage is of relatively low diversity and abundance and is dominated by stratigraphically long-ranging forms which are known from the upper Campanian and Maastrichtian. In terms of the micromorphic brachiopod zonation of the Danish chalk (Surlyk, 1972, 1984), the assemblage studied herein is best comparable to the brachiopod assemblage from the *Rugia tenuicostata*–*Meonia semiglobularis* Zone

(= *tenuicostata-semiglobularis* Zone in Surlyk, 1984, abbreviated *t-s*, referred also to as Zone 7 in Surlyk, 1970). The base of this zone was defined by Surlyk (1984) by the last occurrence of *Rugia tenuicostata* Steinich, 1963, and the top by the appearance of *Meonia semiglobularis* (Posselt, 1894). Both these morphologically distinctive species are absent at Chełm (Fig. 2; Table 1). The stratotype of the *Rugia tenuicostata*–*Meonia semiglobularis* Zone is sample 82 from the Hemmoor section, northern Germany, corresponding to the upper lower Maastrichtian part of the Hemmoor succession (Surlyk, 1984).

Schulz & Schmid (1983, Fig. 3) correlated Zone 7 of Surlyk (1970), that is, the *Rugia tenuicostata*–*Meonia semiglobularis* Zone of Surlyk (1984), with the upper lower Maastrichtian belemnite *Belemnella cimbrica* and *B. fastigata* zones, making the appearance of *Meonia semiglobularis*, a marker for the higher Zone 8 of Surlyk, just beneath marl layer M-900. This bed has been selected as the conventional boundary between the lower and upper Maastrichtian at Hemmoor (e.g., Schulz & Schmid, 1983; Christensen et al., 2005). The same upper lower Maastrichtian position of Zone 7 is presented by Reich & Frenzel (2002, Fig. 7) for the Maastrichtian chalk succession of the Isle of Rügen, northeast Germany. In contrast, the Chełm assemblage is recorded from the lower upper Maastrichtian *Spyridoceramus tegulatus*–*Belemnitella junior* Zone *sensu* Schulz & Schmid (1983), so comes from the Chełm equivalents of Zone 8 at Hemmoor. On the other hand, the lower upper Maastrichtian position of the *Rugia tenuicostata*–*Meonia semiglobularis* Zone is suggested on the log of Stevns 1 borehole by Surlyk et al., (2013, appendix 2). The problem of apparent diachroneity of various biostratigraphical markers in the Boreal Maastrichtian of Europe is beyond the scope of the present work.

Palaeoecology

Except for burrowing *Lingula*, all brachiopods from the European white chalk in general, and from the Chełm succession in particular, represent a guild of fixo- and libero-sessile epifaunal suspension feeders as distinguished by Engelke et al., (2016, 2017) in their study of early Maastrichtian macrobenthos at Kroonsmoor, northwest Germany. In view of the ecological requirements of this group, the development of the Late Cretaceous brachiopod communities in the Boreal Chalk Sea of Europe must have been controlled largely by two interrelated environmental factors: 1) input of food and nutrients, and 2) availability of minute skeletal substrates which would have been suitable for brachiopod settlement (Surlyk, 1972; Hansen & Surlyk, 2014; Engelke et al., 2016, 2017). Both factors were, in turn, indirectly influenced by the depth of the Boreal Chalk Sea and its variations (e.g., Hansen & Surlyk, 2014). The substrate–brachiopod relationship is easiest to grasp based on simple geological and palaeontological evidence and is considered in more detail below.

According to Schröder & Surlyk (2020), the white chalk brachiopods may be subdivided into seven groups in terms of their adaptations and strategies to live on the sea bottom. Based on that paper, we characterise these groups as follows: 1) micromorphic species attached with a pedicle and able to use very small, hard substrates; 2) medium- to large-sized species attached with a pedicle to large, hard substrates; 3) species attached directly to the soft sediment with a rootlet pedicle; 4) secondarily free-living pedunculate species, attached to the substrate by pedicle at the juvenile stages; 5) species attached by cementation by the whole surface of the ventral valve; 6) species attached by cementation in the juvenile stage, but secondarily free-living in the adult stage,

therefore possessing a small attachment surface on the ventral valve; and 7) species burrowed into the soft-bottom substrate. Table 1 presents the assignment of the brachiopod taxa from Chełm to these categories along their relative abundance. Except for group 5, all the groups distinguished by Schröder & Surlyk (2020) are present in the Chełm material, with a clear predominance of group 1 (Table 1).

As demonstrated by Surlyk (1972, Fig. 3), there is a striking parallelism between the washing residue curve (approximately corresponding to the bryozoan curve) and the curves illustrating the brachiopod species and specimen-abundance throughout the Danish chalk succession (see also Surlyk & Birkelund, 1977). According to these authors, the low brachiopod diversity and abundance in the upper lower and lower upper Maastrichtian assemblages, including that from the *Rugia tenuicostata*–*Meonia semiglobularis* Zone, resulted from low availability of substrates suitable for colonisation by brachiopods on the sea floor, reflected in low numbers of skeletal hash, mainly bryozoans, in the washed residues. In contrast, the lower lower and uppermost Maastrichtian maxima in brachiopod diversity and abundance reflect a superabundance of predominantly bryozoan hash on the sea bottom, discernible as relevant peaks in washing residues (Surlyk, 1972, Fig. 3). The three curves seem, in turn, to be indirectly related to bathymetry, with depauperate brachiopod communities linked to the deeper-water portions of the chalk succession (Surlyk, 1972; see also Hansen & Surlyk, 2014).

The brachiopod assemblage from the Chełm succession matches the above observations, as the Chełm chalk represents a relatively deep-water, ‘benthos-poor’ subfacies of the white chalk (Machalski et al., 2021), characterised by a paucity of minute skeletal substrates on the sea floor. Minor variations in brachiopod diversity and abundance at Chełm (Fig. 2) are not easy to explain with the evidence at hand. The differences in diversity may simply result from sampling bias, but the highest abundance at level III (Fig. 2) may reflect a temporal improvement of environmental conditions on the sea floor. Notably, an increase in abundance of epifaunal suspension-feeding bivalves has been recorded from that level by Machalski et al., (2021, Supplementary Information). Minor temperature variations inferred from oxygen stable isotopic analyses of benthic foraminiferal tests from Chełm (Machalski et al., 2021, Fig. 2) are not correlatable in any way with the changes in brachiopod abundance reported herein.

Conclusions

- A brachiopod assemblage is described for the first time from the lower upper Maastrichtian (Upper Cretaceous) white chalk succession exposed at Chełm, eastern Poland.
- The assemblage comprises 15 species in total, with taxonomic diversity and specimen abundance varying between the samples studied.
- The brachiopod assemblage from Chełm is relatively poor in terms of taxonomic diversity and specimen abundance and is dominated by stratigraphically long-ranging species.
- In terms of the micromorphic brachiopod zonation of the European Boreal chalk succession, the brachiopod assemblage from Chełm is best comparable to that from the *Rugia tenuicostata*–*Meonia semiglobularis* Zone as distinguished in the white chalk successions in Denmark and northern Germany, although this zone is usually placed there in the upper lower Maastrichtian.
- The brachiopod assemblage studied is typical of a relatively deep-water and ‘benthos-poor’ subfacies of white chalk of the

Boreal Chalk Sea, the Chelm chalk belongs to; its development seems to have been controlled largely by a low availability of minute skeletal substrates suitable for brachiopod settlement.

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References

- Bitner, M.A. & Pisera, A.**, 1979. Brachiopods from the Upper Cretaceous chalk of Mielnik. *Acta Geologica Polonica* **29**: 67–88.
- Błaszkiewicz, A.**, 1980. Campanian and Maastrichtian ammonites of the Middle Vistula River Valley, Poland: a stratigraphic-paleontological study. *Prace Instytutu Geologicznego* **92**: 1–63.
- Bojanowski, M.J., Dubicka, Z., Minoletti, F., Olszewska-Nejbert, D. & Surowski, M.**, 2017. Stable C and O isotopic study of the Campanian chalk from the Mielnik section (eastern Poland): signals from bulk rock, belemnites, benthic foraminifera, nannofossils and microcrystalline cements. *Palaeogeography, Palaeoclimatology, Palaeoecology* **465**: 193–211. DOI: [10.1016/j.palaeo.2016.10.032](https://doi.org/10.1016/j.palaeo.2016.10.032).
- Christensen, W.K., Schmid, F. & Schulz, M.-G.**, 2005. *Belemnitella* from the Upper Maastrichtian of Hemmoor, Northwest Germany. *Geologisches Jahrbuch A157*(for 2004): 23–67.
- Dubicka, Z. & Peryt, D.**, 2011. Integrated biostratigraphy of Upper Maastrichtian chalk at Chelm (SE Poland). *Annales Societatis Geologorum Poloniae* **81**: 185–197.
- Dubicka, Z. & Peryt, D.**, 2012. Latest Campanian and Maastrichtian paleoenvironmental changes: implications from an epicontinental sea (SE Poland and western Ukraine). *Cretaceous Research* **37**: 272–284. DOI: [10.1016/j.cretres.2012.04.009](https://doi.org/10.1016/j.cretres.2012.04.009).
- Emig, C.C.**, 1990. Examples of post-mortality alternation in recent brachiopod shells and (paleo)ecological consequences. *Marine Biology* **104**: 233–238.
- Engelke, J., Esser, K.J.K., Linnert, C., Mutterlose, J. & Wilmsen, M.**, 2016. The benthic macrofauna from the Lower Maastrichtian chalk of Kronsmoor (northern Germany, Saturn quarry): taxonomic outline and palaeoecologic implications. *Acta Geologica Polonica* **66**: 671–694.
- Engelke, J., Linnert, C., Mutterlose, J. & Wilmsen, M.**, 2017. Early Maastrichtian benthos of the chalk at Kronsmoor, northern Germany: implications for Late Cretaceous environmental change. *Palaeobiodiversity and Palaeoenvironments* **97**: 703–722.
- Ernst, H.**, 1984. Ontogenie, Phylogenie und Autökologie des inarticulaten Brachiopoden *Isocrania* in der Schreibkreidefazies NW-Deutschlands (Coniac bis Maastricht). *Geologisches Jahrbuch A77*: 3–105.
- Hagenow, F. von**, 1842. Monographie der Rugen'schen Kreide-Versteinerungen III. Abtheilung: Mollusken. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie, und Petrefakten-Kunde* **1842**: 528–579.
- Hansen, T. & Surlyk, F.**, 2014. Marine macrofossil communities in the uppermost Maastrichtian chalk of Stevns Klint, Denmark. *Palaeogeography, Palaeoclimatology, Palaeoecology* **399**: 323–344.
- Jelby, M.E., Thibault, N.R., Surlyk, F., Ullmann, C.V., Harlou, R. & Korte, C.**, 2014. The lower Maastrichtian Hvidskud succession, Møns Klint, Denmark: calcareous nannofossil biostratigraphy, carbon isotope stratigraphy, and bulk and brachiopod oxygen isotopes. *Bulletin of the Geological Society of Denmark* **62**: 89–104.
- Johansen, M.B.**, 1987a. Brachiopods from the Maastrichtian-Danian boundary sequence at Nye Kløv, Jylland, Denmark. *Fossils & Strata* **20**: 1–100.
- Johansen, M.B.**, 1987b. The micromorphic brachiopod genus *Rugia* Steinich from the Middle Coniacian-Lower Maastrichtian chalk of Lägerdorf and Kronsmoor, northwest Germany. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* **63**: 127–183.
- Johansen, M.B. & Surlyk, F.**, 1990. Brachiopods and the stratigraphy of the Upper Campanian and Lower Maastrichtian chalk of Norfolk, England. *Palaeontology* **33**: 823–872.
- Kowalewski, M. & Flessa, K.W.**, 1996. Improving with age: the fossil record of lingulide brachiopods and the nature of taphonomic megabiases. *Geology* **24**: 977–980.
- Lundgren, B.**, 1885. Undersökningar öfver Brachiopoderna i Sverges kritsystem. *Årsskrift Lunds Universitet* **20**: 1–72.
- Machalski, M.**, 2005. Late Maastrichtian and earliest Danian scaphitid ammonites in central Europe: taxonomy, evolution, and extinction. *Acta Palaeontologica Polonica* **50**: 653–696.
- Machalski, M., Owocki, K., Dubicka, Z., Malchuk, O. & Wierny, W.**, 2021. Stable isotopes and predation marks shed new light on ammonoid habitat depth preferences. *Scientific Reports* **11**(1): 22730. DOI: [10.1038/s41598-021-02236-9](https://doi.org/10.1038/s41598-021-02236-9).
- MacKinnon, D.I., Simon, E. & Bitner, M.A.**, 1998. A reappraisal of the problematic European, Late Cretaceous brachiopod *Leptothyrellopsis polonicus* Bitner & Pisera, 1979. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* **68**: 175–180.
- Naidin, D.P.**, 1952. Upper Cretaceous belemnites of western Ukraine. *Trudy Moskovskogo Geologicheskogo Razvedochnogo Instituta imeni S. Ordzhonikidze*, vol. **27**: 1–170, [In Russian].
- Nowak, J.**, 1913. Untersuchungen über die Cephalopoden der oberen Kreide in Polen. III Teil. *Bulletin de l'Académie des Sciences de Cracovie. Classe des Sciences Mathématique et Naturelles. Série B. Sciences Naturelles* **335**: 1913–1415.
- Posselt, H.J.**, 1894. Brachiopoderne i den danske Kridtformation. *Danmarks Geologiske Undersøgelse, Second Series* **4**: 1–59.
- Reich, M. & Frenzel, P.**, 2002. Die Fauna und Flora der Rügiger Schreibkreide (Maastrichtium, Ostsee). *Archiv für Geschiebekunde* **3**: 73–284.
- Roemer, A.**, 1841. Die Versteinerungen des norddeutschen Kreidegebirges. Hannover, 1–145.
- Schlothheim, E.F. von**, 1813. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. Leonhard's Taschenbuch für die gesammte Mineralogie **7**: 1–134.
- Schröder, A.E. & Surlyk, F.**, 2020. Adaptive brachiopod morphologies in four key environments of the Late Cretaceous-Danian Chalk Sea of northern Europe: a comparative study. *Cretaceous Research* **107**: 104288. DOI: [10.1016/j.cretres.2019.104288](https://doi.org/10.1016/j.cretres.2019.104288).
- Schulz, M.-G. & Schmid, F.**, 1983. Das Ober-Maastricht von Hemmoor (N-Deutschland): Faunenzonen-Gliederung und Korrelation mit dem Ober-Maastricht von Dänemark und Limburg. *Newsletters on Stratigraphy* **13**: 203–215.
- Simon, E. & Mottequin, B.**, 2018. Extreme reduction of morphological characters: a type of brachidial development found in several Late Cretaceous and Recent brachiopod species – new relationships between taxa previously listed as *incertae sedis*. *Zootaxa* **4444**(1): 001–024.
- Sowerby, C. de**, 1823. Genera of recent and fossil shells. 4. Sherwood and Co, London, pp. 115–160.
- Steinich, G.**, 1963. Drei neue Brachiopodengattungen der Subfamilie Cancellothyridinae Thomson. *Geologie* **12**(6): 732–740.
- Steinich, G.**, 1965. Die artikulaten Brachiopoden der Rügiger Schreibkreide (Unter-Maastricht). *Paläontologische Abhandlungen, Abteilung A, Paläozoologie* **2**: 1–220.
- Surlyk, F.**, 1970. Die Stratigraphie des Maastricht von Dänemark und Norddeutschland aufgrund von Brachiopoden. *Newsletters on Stratigraphy* **12**: 7–16.
- Surlyk, F.**, 1972. Morphological adaptation and population structures of the Danish chalk brachiopods (Maastrichtian, Upper Cretaceous). *Det Kongelige Danske Videnskabernes Selskab. Biologiske Skrifter* **19**: 1–67.
- Surlyk, F.**, 1982. Brachiopods from the Campanian-Maastrichtian boundary sequence, Kronsmoor (NW Germany). *Geologisches Jahrbuch A61*: 259–277.
- Surlyk, F.**, 1984. The Maastrichtian Stage in NW Europe, and its brachiopod zonation. *Bulletin of the Geological Society of Denmark* **33**: 217–224.
- Surlyk, F. & Birkelund, T.**, 1977. An integrated stratigraphical study of fossil assemblages from the Maastrichtian White Chalk of northwestern Europe. In: Kauffman E.G. & Hazel J.E. (eds): *Concepts and Methods in Biostratigraphy*. Hitchinson and Ross Inc. (Stroudsbouhrg, PA): 257–281.

- Surlyk, F., Dons, T., Clausen, C.K. & Higham, J.**, 2003. Upper Cretaceous. In: *The Millennium Atlas: petroleum geology of the central and northern North Sea*. Geological Society of London: 213–233.
- Surlyk, F., Rasmussen, S.L., Boussaha, M., Schiøler, P., Schovsbo, N.H., Sheldon, E., Stemmerik, L. & Thibault, N.R.**, 2013. Upper Campanian-Maastrichtian holostatigraphy of the eastern Danish Basin. *Cretaceous Research* **46**: 232–256.
- Thibault, N., Harlou, R., Schovsbo, N., Schiøler, P., Minoletti, F., Galbrun, B., Lauridsen, B.W., Sheldon, E., Stemmerik, L. & Surlyk, F.**, 2012. Upper Campanian-Maastrichtian nannofossil biostratigraphy and high-resolution carbon-isotope stratigraphy of the Danish Basin: towards a standard $\delta^{13}\text{C}$ curve for the Boreal Realm. *Cretaceous Research* **33**: 72–90.
- Walaszczyk, I., Dubicka, Z., Olszewska-Nejbert, D. & Remin, Z.**, 2016. Integrated biostratigraphy of the Santonian through Maastrichtian (Upper Cretaceous) of extra-Carpathian Poland. *Acta Geologica Polonica* **66**: 321–358.
- Walaszczyk, I., Jagt, J.W.M. & Keutgen, N.**, 2010. The youngest Maastrichtian ‘true’ inoceramids from the Vijlen Member (Gulpen Formation) in northeastern Belgium and the Aaschen area (Germany). *Netherlands Journal of Geosciences* **89**(2): 147–167.