# The benthic macrofauna from the Lower Maastrichtian chalk of Kronsmoor (northern Germany, Saturn quarry): taxonomic outline and palaeoecologic implications

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ABSTRACT:

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The benthic macroinvertebrates of the Lower Maastrichtian chalk of Saturn quarry at Kronsmoor (northern Germany) have been studied taxonomically based on more than 1,000 specimens. Two successive benthic macrofossil assemblages were recognised: the lower interval in the upper part of the Kronsmoor Formation (*Belemnella obtusa* Zone) is characterized by low abundances of macroinvertebrates while the upper interval in the uppermost Kronsmoor and lowermost Hemmoor formations (lower to middle *Belemnella sumensis* Zone) shows a high macroinvertebrate abundance (eight times more than in the *B. obtusa* Zone) and a conspicuous dominance of brachiopods. The palaeoecological analysis of these two assemblages indicates the presence of eight different guilds, of which epifaunal suspension feeders (fixo-sessile and libero-sessile guilds), comprising approximately half of the trophic nucleus of the lower interval, increased to a dominant 86% in the upper interval, including a considerable proportion of rhynchonelliform brachiopods. It is tempting to relate this shift from the lower to the upper interval to an increase in nutrient supply and/or a shallowing of the depositional environment but further data including geochemical proxies are needed to fully understand the macrofossil distribution patterns in the Lower Maastrichtian of Kronsmoor.

Keywords: Cretaceous; Maastrichtian; Northern Germany; Benthic macrofauna; Taxonomy; Palaeoecology.

## INTRODUCTION

The Late Cretaceous Epoch was characterized by a major global transgression and sea-level highstand resulting in the formation of large peri- and epicontinental shelf seas and the accumulation of widespread (hemi-)pelagic calcareous deposits (Hancock and Kauffmann 1979; Hancock 1989). In north-western Europe, this development created the Chalk Sea, extending as a broad temperate epicontinental facies belt from east of the British Islands between Baltica and the Mid-European Island eastwards into Poland and beyond (Text-fig. 1). Similar chalk facies can be traced further eastward along the northern Tethyan margin at least into the Transcaspian

area. The reasons for the onset of the widespread Late Cretaceous chalk deposition are still controversial. A massive rise of sea-level, changes in ocean circulation and ocean chemistry, as well as evolutionary developments, probably contributed to the specific chalk setting (e.g., Hay 1995, 2008; Stanley *et al.* 2005; Giorgioni *et al.* 2015).

Today, the relatively small shelf seas are characterized by high biological productivity (e.g., Falkowski *et al.* 1998; Thomas *et al.* 2004), suggesting that primary productivity in shelf seas should have been even more important during greenhouse worlds of the geological past when large, shallow epicontinental seas, such as the Late Cretaceous Chalk Sea, existed. During the Late Cretaceous, it is probable that no boundaries were present between the shelf areas and the pelagic realm (shelf fronts) due to high sea-level stands (Hay 1995, 2008), in contrast to the present-day situation. Typical sediments of Late Cretaceous temperate to Boreal shelf areas are thus pelagic carbonates (calcareous nannofossils and foraminiferal ooze, i.e. chalks). Today, comparable sediments are deposited in open oceanic settings.

The structure of fossil food chains in pre-Cenozoic oceans is poorly understood. This is especially true for the food chain of the Cretaceous Chalk Sea due to the lack of high-resolution quantitative integrated palaeobiological, palaeoecological and geochemical data. The Upper Campanian to Lower Maastrichtian strata of the Kronsmoor section in Germany offer an undisturbed succession of chalks and a unique opportunity to com-pile an integrated data set in search for clues to the pelagic-benthic coupling and to the palaeoceanography of the Chalk Sea. The scope of the present paper is to provide an account of the taxonomy of the benthic macrofauna and to discuss its palaeoecology, abundance and diversity in the Lower Maastrichtian part of the Kronsmoor section.
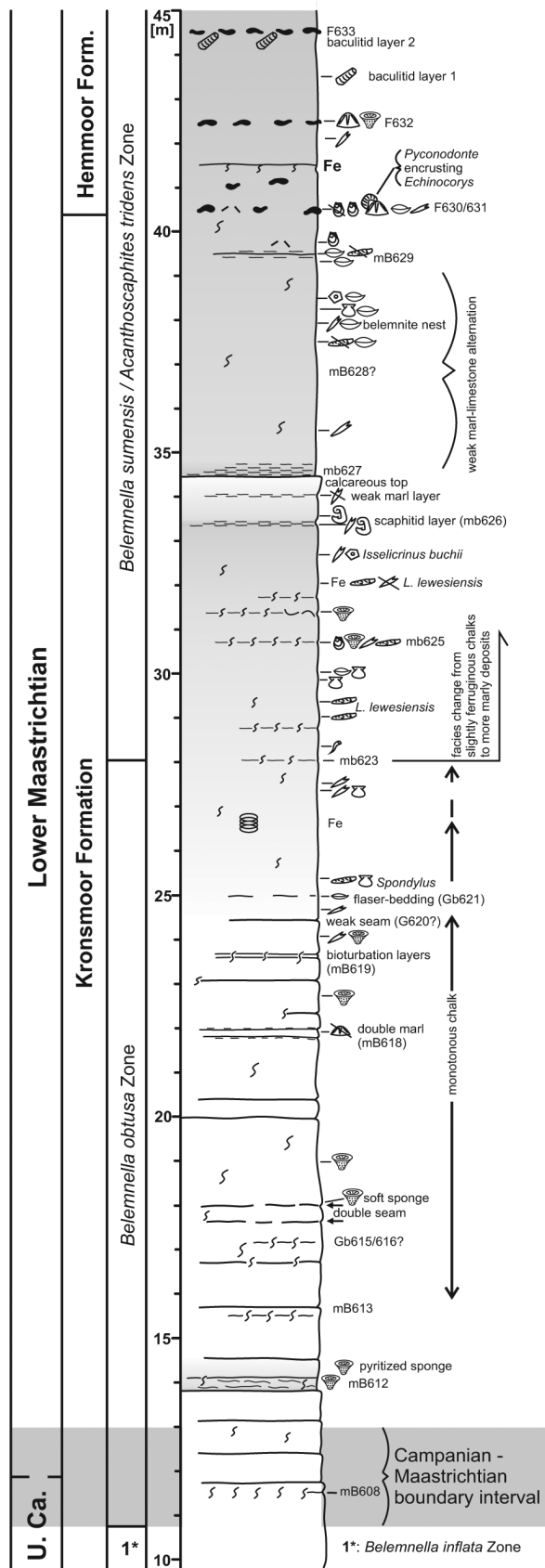
GEOLOGICAL SETTING

The northern German shelf was part of the southern margin of the North Sea Basin, a shallow epicontinental sea located in the Boreal Realm (Text-fig. 1A). During Campanian to Maastrichtian times, the study area was situated close to the centre of the North Sea Basin (Text-fig. 1A). Terrigenous input was low due to the considerable distance to potential source areas. The water depth of the Chalk Sea has been variably interpreted (e.g., Trusheim 1936; Ernst 1978; Hancock 1989), but its floor was, in wide areas, certainly below maximum storm-wave base and the base of the euphotic zone (e.g., Ineson *et al.* 2005). The water depth may have ranged between 50 m and 200–300 m (e.g., Nestler 1965; Ernst 1978).

The Saturn quarry near Kronsmoor is situated ca. 50 km north-northwest of Hamburg (Text-fig. 1B). The section is part of the so-called Lägerdorf-Kronsmoor-Hemmoor chalk standard section of northern Germany, ranging stratigraphically from the Middle Coniacian
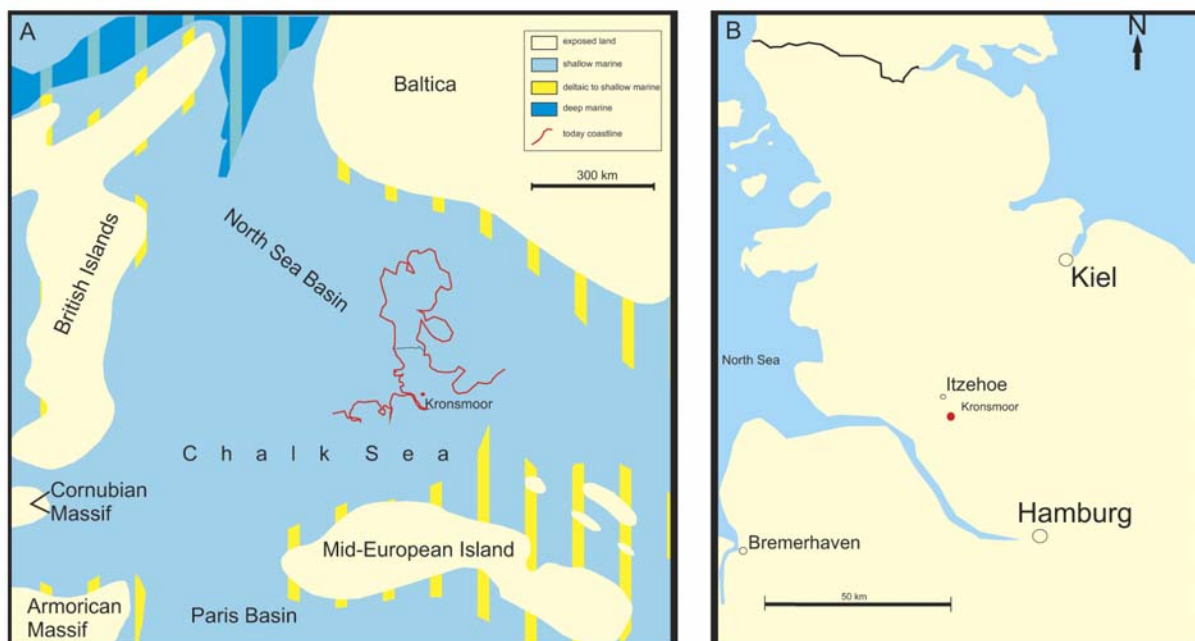


Text-fig. 1. A – Palaeogeographic map of the Late Cretaceous Chalk Sea during the Cenomanian to Maastrichtian, modified after (Vejbæk *et al.* 2010); B – Map of northern Germany showing the position of the Kronsmoor section (red dot)

Text-fig. 2. The 35-meter thick target interval from the Kronsmoor and Hemmoor formations (lower Maastrichtian) of Saturn quarry

into the Upper Maastrichtian (Ernst and Schulz 1974; Schulz *et al.* 1984; Schönfeld *et al.* 1996; Niebuhr 2006). The several hundred-metres-thick stratal succession has already been uplifted by the northeast–southwest-elongated salt structure of Krempe (e.g. Schulz and Weitschat 1998). This salt structure had its main activity during the Late Triassic to Jurassic and is part of the Glückstadt Graben system, the inversion of which occurred during the Cenozoic (Baldschuhn *et al.* 1991; Baldschuhn *et al.* 2001; Maystrenko *et al.* 2005). The total thickness of the Kronsmoor section is 100 m and it offers a continuous succession of the upper Upper Campanian to lower Lower Maastrichtian Kronsmoor Formation (Niebuhr 2006). It is an essentially flintless succession of soft chalks, underlain by the flint-bearing uppermost Lower to upper Upper Campanian Dägeling Formation and overlain by the flint-rich upper Lower to lower Upper Maastrichtian Hemmoor Formation.

Numerous geological papers have been published on the Upper Cretaceous chalks of the Lägerdorf–Kronsmoor area, and only a few can be mentioned here that are of crucial importance for the present study. Different groups of macro- and microfossils have already been monographed: benthic foraminifera (Schönfeld 1990), serpulids (Jäger 2004), brachiopods (Surlyk 1982), with Ernst (1984) focussing on *Isocrania*, ammonites (Niebuhr 2003), nautilids (Wilmsen and Esser 2004) and belemnites (Schulz 1982). Biostratigraphic zonation and lithological descriptions were compiled by Ernst (1963), Schulz (1978), Schulz *et al.* (1984), Schönfeld *et al.* (1996) and Niebuhr (2006). McArthur *et al.* (1992) provided the strontium isotope stratigraphy of the Kronsmoor section and discussed the Campan-

ian–Maastrichtian boundary (placed at flint layer F600 at that time). However, the position of the Campanian–Maastrichtian boundary has been revised by Niebuhr *et al.* (2011) and placed ca. 10 m above the old boundary at the base of the *Belemnella obtusa* Zone.

Ehrmann (1986) used the Lägerdorf–Kronsmoor–Hemmoor standard section to estimate accumulation rates of the north German chalk (mean ~24.5 m/ma). Carbon and oxygen stable isotope data of the Kronsmoor Formation are available through the studies of Friedrich *et al.* (2005), Voigt *et al.* (2010) and Niebuhr *et al.* (2011). Voigt and Schönfeld (2010) suggested an astronomical time scale for the Late Campanian–Early Maastrichtian based on time-series analyses of carbonate content. Recently, Linnert *et al.* (2016) studied the nannofossils from the target interval with high resolution sampling (each 25 cm).

The Lower Maastrichtian target interval, studied here, has a thickness of 35 m (Text-fig. 2) and ranges from the *Belemnella obtusa* Zone into the *Belemnella sumensis* Zone (Niebuhr *et al.* 2011). It comprises the upper part of the Kronsmoor and the lowermost part of the Hemmoor Formation. The lowermost part of the section is characterized by a macrofossil-poor, monotonous chalk facies with few bioturbated horizons. The middle part shows a few chalk-marl cycles, a relative high abundance of macrofossils and a higher degree of bioturbation. The uppermost part (Hemmoor Formation) is characterized by the appearance of flints and comprises three conspicuous flint layers (F630, F632 and F633).

MATERIAL AND METHODS

More than 1,000 benthic macrofossil specimens from the Kronsmoor section have been collected over two decades largely in-situ from the *B. obtusa* to *B. sumensis* Zone by one of the authors (KJKE) in the Saturn quarry (see discussion on suspected sampling bias below). The fossils are stored in the palaeozoology collection of the Senckenberg Naturhistorische Sammlungen Dresden, Museum for mineralogy and geology (MMG), paleozoology section (repository ShK). The material consists of 145 bivalve, 41 gastropod (only steinkern preservation), 548 brachiopod, 96 irregular echinoid, 49 regular echinoid, 70 crinoid, three asteroid, seven serpulid, 25 sponge, 43 coral and three bryozoan specimens. Additional material has been collected during field campaigns in April and August 2014 and in

May 2015. The fossils have been mechanically cleaned using brushes and soft abrasives. In total, more than 50 taxa have been identified, the most important and common of which are briefly described and illustrated in the systematic chapter below. For the open nomenclature, we follow Bengtson (1988).

RESULTS

**Benthic macrofauna**

This chapter is a short taxonomic account that deals with the most important benthic macrofossils from the Lower Maastrichtian of Kronsmoor, which are briefly described and illustrated. The listed occurrences only refer to the stratigraphic ranges in the studied section.

**Bivalves**. Bivalves are a main fossil group in Cretaceous shelf deposits in terms of abundance as well as ecological and taxonomic diversity. For more details on Boreal Upper Cretaceous bivalves, see e.g. Dhondt (1971, 1972, 1982), Carter (1972), Pugaczewska (1977), Abdel-Gawad (1986), Dhondt and Jagt (1987), Cleevely and Morris (2002) and Niebuhr *et al.* (2014, further references therein).

*Pycnodonte* (*Phygraea*) *versicularis* (Lamarck, 1806); Text-fig. 3A1, 3A2; 47 specimens from the *B. obtusa* to *B. sumensis* zones (very common in *B. sumensis* Zone): These large oysters (up to 150 mm in height), are mostly preserved with both valves articulated. The left valve is strongly convex, the right valve concave and semi-circular. The outline is rounded to oval, the shell thick-walled, with the vesicular layer present. Encrusting bryozoans and serpulids are common. In some cases, *Pycnodonte versicularis* has been found encrusting on coronas of *Echinocorys* or *Galerites*.

*Hyotissa semiplana* (Sowerby, 1925); Text-fig. 3E1, 3E2; 12 specimens from the *B. sumensis* Zone (common in the interval from mB628–F631): This is a medium-sized oyster (up to 40 mm in height), lunate to very variable in outline, with eight distinctive ribs or folds. The shell has a vesicular wall structure, mostly only one valve is present.

*Neithea sexcostata* (Woodward, 1833); Text-fig. 3B; four specimens from the *B. sumensis* Zone (mB628–F630):

Text-fig. 3. Bivalves. **A** – *Pycnodonte* (*Phygraea*) *vesicularis* (Lamarck, 1806), ShK 65, natural size, **A1** right valve, **A2** left valve. **B** – *Neithea sexcostata* (Woodward, 1833), ShK 66, × 2, convex valve. **C** – *Entolium* sp., ShK 67, natural size. **D** – *Spondylus spinosus* (Sowerby, 1814), ShK 68, natural size, **D1** right valve, **D2** commissure view. **E** – *Hyotissa semiplana* (Sowerby, 1825), ShK 69, natural size, left valve, **E1** external view, **E2** interior view. **F** – *Lyropecten* sp., ShK 70, × 2. **G** – *Cataceramus* sp., ShK 71, natural size
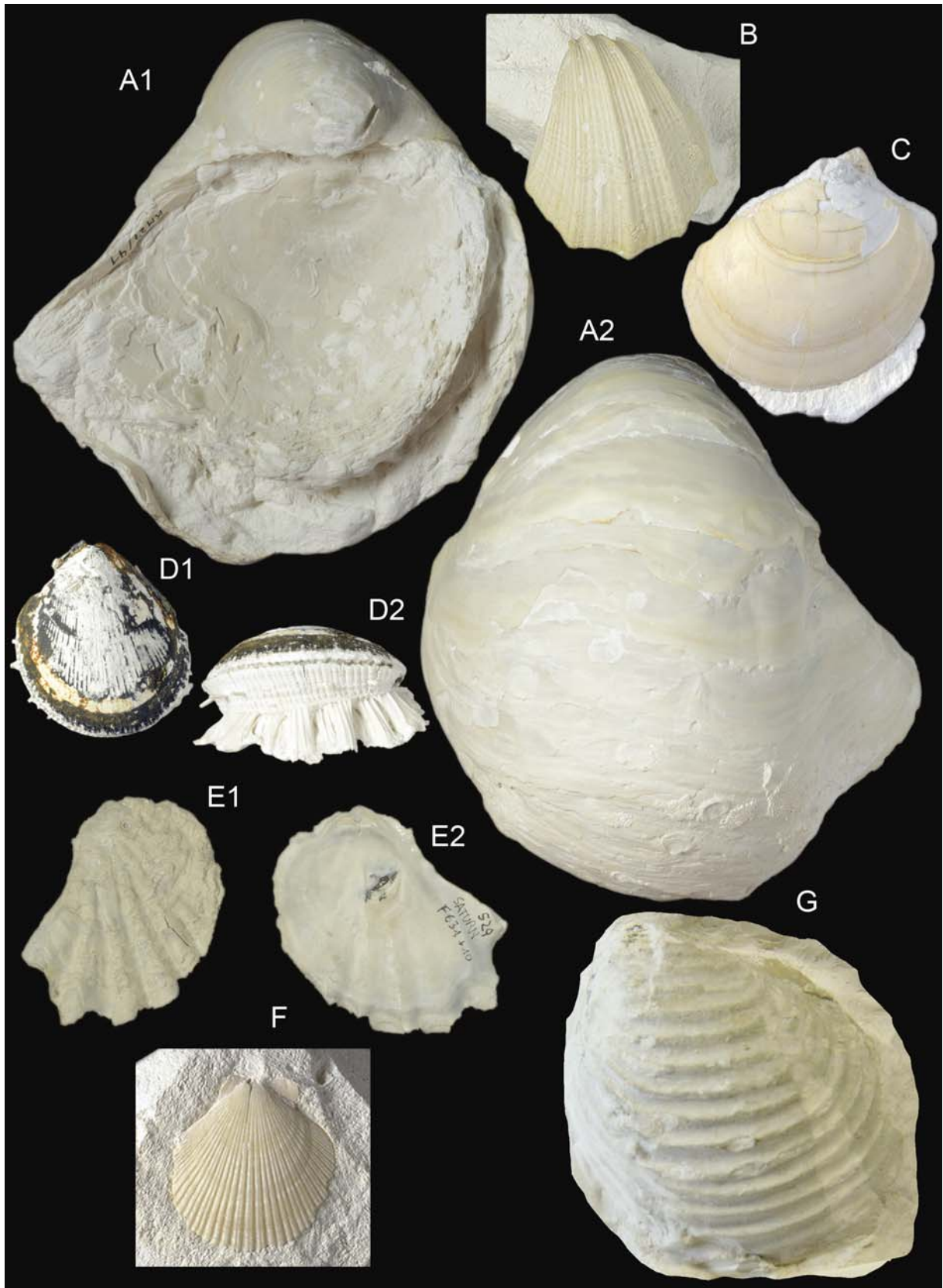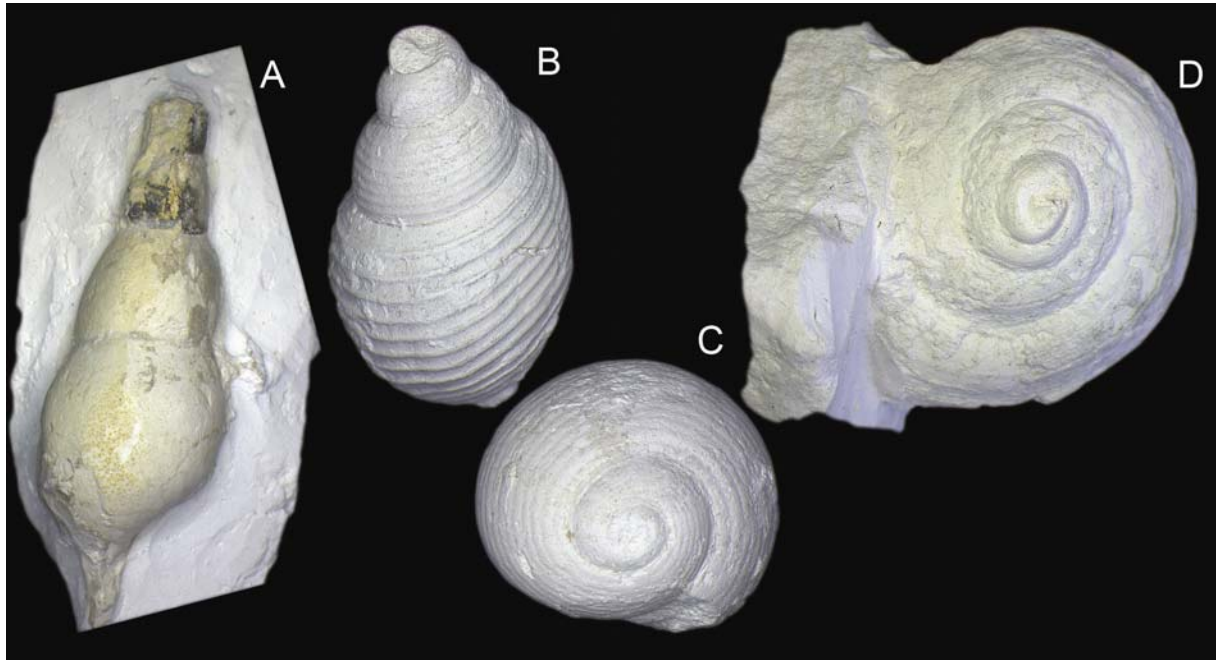
Text-fig. 4. Gastropods (all figures × 2). **A** – Gastropoda indet. a, ShK 72. **B** – Gastropoda indet. b, ShK 73. **C** – Gastropoda indet. c, ShK 74. **D** – Gastropoda indet. d, ShK 75, apical view

This is a small-size *Neithea* (up to 20 mm in height) with six primary ribs and four to five intercalated ribs between each two primary ribs. The right valve is strongly convex and arched. The outline is triangular to ovate. *Neithea sexcostata* differs from *Neithea quinquecostata* in its smaller shell size, its salient primary ribs and the large number of intercalatories (Cleevely and Morris 2002).

*Spondylus spinosus* (Sowerby, 1814); Text-fig. 3D1, 3D2; three specimens from the *B. sumensis* Zone: This is a medium-sized (up to 35 mm in height), bilaterally symmetric and equivalved bivalve with an ovate outline. Both valves are convex with up to 30 fine radial ribs. Spines occur only on the right valve while on the left valve, distinct growth lines are visible. Carter (1972) suggested that the spines on the right valve were an adaption to the epifaunal living mode (snowshoe strategy on a soft substrate rather than defensive devices; see also Niebuhr *et al.* 2014). In recent *Spondylus*, both valves bear spines.

*Lyropecten* sp.; Text-fig. 3F; three specimens from the *B. sumensis* Zone: This is a small pectinid (up to 30 mm in length), with a round outline and bilateral symmetry. It bears numerous rounded, radial ribs, most of them primaries. Anterior and posterior auricles are present, the anterior one being larger.

*Entolium*? sp.; Text-fig. 3C; two specimens from the *B. sumensis* Zone: This thin-shelled entoliid has an oval outline, and, apart from thin growth lines, no ornamentation. The shell is slightly asymmetric, the posterior end is slightly elongated. Due to the slightly asymmetric shell, the generic assignment to *Entolium* is questionable.

Inoceramids were common in the Lower Maastrichtian of Kronsmoor as can be judged from the isolated shell prisms and fragments retrieved from washed samples. Complete shells or internal moulds are rare however, but macrofossil remains are more common in the *B. sumensis* Zone, where there are some large, flat inoceramid shell fragments in bed F630. Walaszczyk *et al.* (2009) provide a recent account of Campanian–Masstrichtian inoceramid bivalves.

*Cataceramus* sp.; Text-fig. 3G; five specimens from the *B. sumensis* Zone: This inequilateral inoceramid bivalve (58 mm in length, 46 mm in height) has a subcircular to subovate outline. The valves are ornamented with regularly spaced commarginal rugae (up to 16).

**Gastropods**. Gastropods are relatively rare in the chalk of Kronsmoor. The exact identification of gastropods is inhibited by the poor steinkern preservation of the Kronsmoor specimens, but seven different morphotypes

are herein differentiated (Gastropoda indet a–g), following e.g. Kutscher (1984). The naticids were not identified as body fossils but were proved by means of their characteristic round boreholes in brachiopods.

Gastropoda indet. a (*Rostellaria*? sp.); Text-fig. 4A; 15 specimens from the *B. sumensis* Zone: This high-spired shell (32 mm in length) possesses four smooth, convex whorls. The apex is not preserved. The general morphology may indicate an affinity to the aporrhaid genus *Rostellaria.*

Gastropoda indet. b (*Fasciolaria*? sp.); Text-fig. 4B; two specimens from the boundary between the *B. obtusa* to *B. sumensis* zones: This is a moderately high (up to 25 mm in length) turbinid shell with three convex whorls carrying eleven distinctive spiral ridges. The apex is not preserved.

Gastropoda indet. c (*Avellana*? sp.); Text-fig. 4C; 16 specimens from the *B. obtusa* to *B. sumensis* zones: This is a small (up to 20 mm in diameter), trochiform gastropod with three whorls and distinctive spiral lines.

Gastropoda indet. d (*Bathrotomaria*? sp.); Text-fig. 4D; two specimens from the *B. obtusa* Zone: The specimens are trochiform with four whorls (up to 25 mm in diameter) and fine spiral lines.

**Brachiopods**. Brachiopods are very common in the Lower Maastrichtian of Kronsmoor, constituting more than 50% of the total macrofauna. For detailed descriptions and identifications of Maastrichtian taxa, see e.g. Johansen and Surlyk (1990) and Reich and Frenzel (2002).

*Isocrania costata* (Sowerby, 1823); Text-fig. 5B1, 5B2; seven specimens from the *B. sumensis* Zone: Only dorsal valves are present. These are convex and show up to 12 primary ribs radiating from the umbo and three to eight intercalated ribs. The shell outline is circular to subrectangular. The shell edge is broad and pustulate. Interior shell features comprise the anterior adductors closely together, the posterior adductors at the valve edge. Ernst (1984) discusses the different morphological adaptions of the *Isocrania costata* and *Isocrania borealis* groups. The *I. borealis* group has a larger attachment surface due to the fact that they lived fixed to a substrate during all their life. The *I. costata* group became free-living in the adult stage.

*Neoliothyrina obesa* (Sahni, 1925); Text-fig. 5J1, 5J2, 5J3; twelve specimens from the *B. sumensis* Zone: This is a medium-sized brachiopod (up to 50 mm in length)

with an oval to trapezoid outline. Both valves are convex and smooth (apart from growth lines). The commissure is paraplicate and the broadly curved umbo is dorsally directed. The foramen is large. Bryozoans are found to encrust its dorsal valve.

*Magas chitoniformis* (Schlotheim, 1813); Text-fig. 5E1, 5E2, 5E3; 158 specimens from the *B. obtusa* to *B. sumensis* zones, with an abundance peak in the uppermost Kronsmoor Formation (mid-*B. sumensis* Zone): This small brachiopod (commonly 10 mm in length and 10 mm in width) has a planoconvex shell (dorsal valve flat, ventral valve convex). Its outline is circular and both valves show conspicuous growth lines. The commissure is generally rectimarginate to low unisulcate, the beak is strongly curved.

*Trigonosemus pulchellus* (Nilsson, 1827); Text-fig. 5G1, 5G2, 5G3; 21 specimens from the *B. sumensis* Zone: This small brachiopod (commonly 13 mm in length and 12 mm in width) possesses distinctive radial ribs (15 to 25 primary, six to ten intercalated ribs) crossed by conspicuous growth lines. The ventral valve is convex, the smaller dorsal valve flat to low convex (planoconvex shell), the commissure unisulcate. The umbo is strongly curved with the beak pointed anterodorsally.

*Carneithyris subcardinalis* (Sahni, 1925); Text-fig. 5F1, 5F2, 5F3; 159 specimens from the *B. obtusa* to *B. sumensis* zones: This is a medium-sized brachiopod (26 mm in length) with a low-biconvex shell and nearly circular outline. The umbo is small and the beak is curved (suberect) with a small foramen. The commissure is rectimarginate. The ornament is composed exclusively of growth lines.

*Carneithyris* sp.; Text-fig. 5D1, 5D2, 5D3; two specimens from the *B. sumensis* Zone: This is a medium-sized, biconvex brachiopod (commonly 29 mm in length and 22 mm in width) with elongate outline and rectimarginate commissure. The shell is smooth with conspicuous growth lines (up to 20). The umbo is short, curved, with erect beak and small foramen. *Carneithyris* sp. differs from *Carneithyris subcardinalis* in its elongate outline and larger shell size; the early growth stages of both forms are similar. Consequently, it is possible that *Carneithyris subcardinalis* is only the juvenile of *Carneithyris* sp. and both taxa are conspecific, and should be classified as *Carneithyris subcardinalis*. Some specimens bear rounded borings with inward-inclined smooth walls which are evidence of predation by naticid gastropods.
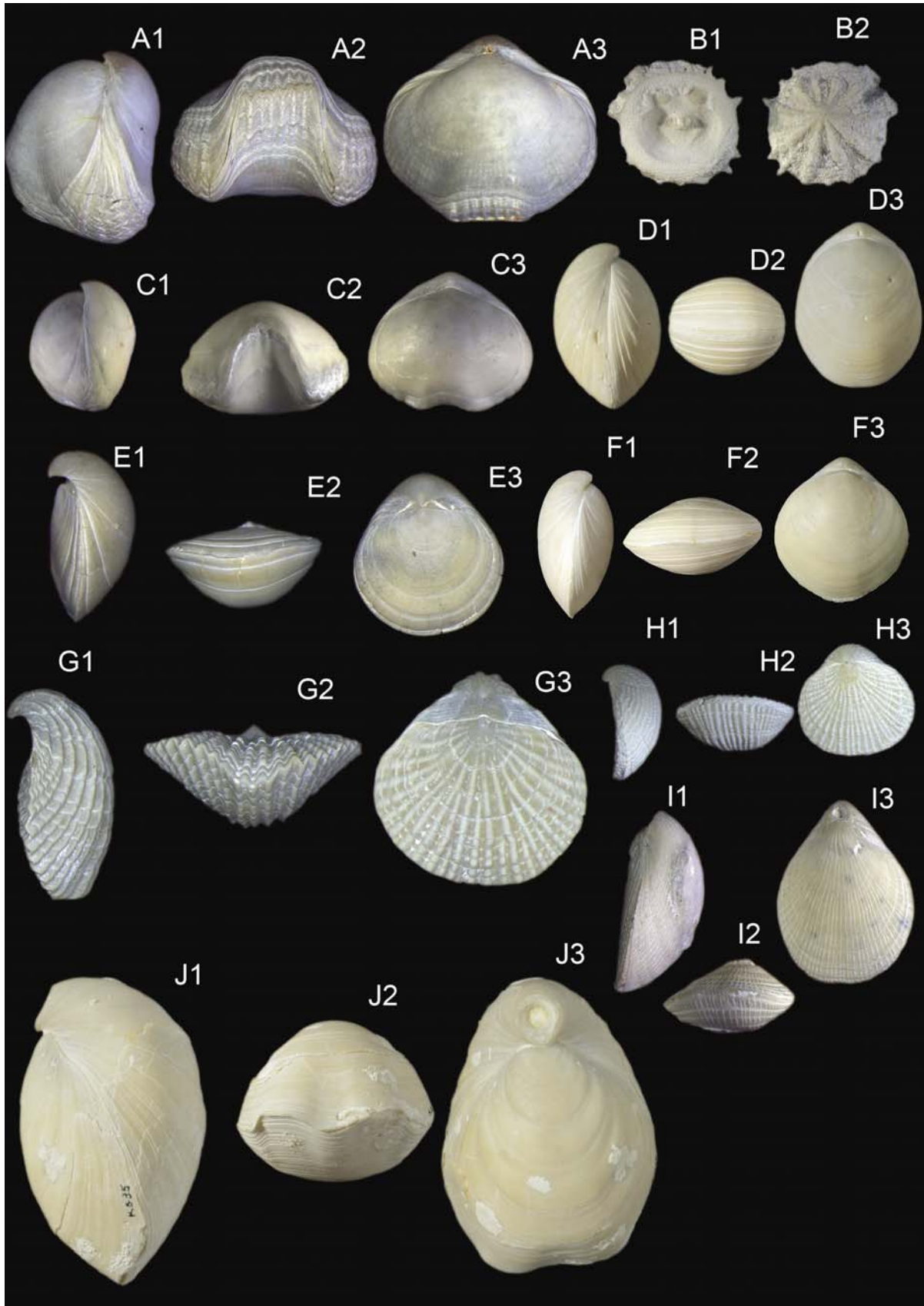
*Terebratulina chrysalis* (Schlotheim, 1813); Text-fig. 5I1, 5I2, 5I3; 49 specimens from the *B. obtusa* to *B. sumensis* zones: This small brachiopod (commonly 11 mm in length and 8 mm in width) is elongate with an oval outline and a planoconvex to concavoconvex shell. The ornament is composed of numerous fine radial ribs and growth lines. The commissure is rectimarginate.

*Gyrosoria gracilis* (Schlotheim, 1813); Text-fig. 5H1, 5H2, 5H3; eight specimens from the *B. sumensis* Zone: This is a small-sized brachiopod (commonly 7.4 mm in length and 7.6 mm in width) with a planoconvex to concavoconvex shell and circular outline. The ornament consists of distinctive ribbing with up to 30 primary and 12 secondary ribs crossed by growth lines. The lateral profile is hemispherical, the commissure retimarginate to parasulcate, and the beak strongly curved. Sklenář and Simon (2009) assigned *Terebratulina gracilis* to the genus *Gyrosoria* Cooper.

*Cretirhynchia retracta* (Roemer, 1841); Text-fig. 5A1, 5A2, 5A3; 95 specimens from the *B. obtusa* to *B. sumensis* zones: This medium-sized brachiopod (commonly 12 mm in length) possesses a fold in the dorsal and a sulcus in the ventral valve and is transversely oval in outline. The shell is unequally biconvex; the dorsal valve is more convex than the ventral one. The commissure is uniplicate with a zigzac pattern. The umbo is small and the beak suberect with small circular foramen. A recent taxonomic revision of the genus *Cretirhynchia* was provided by Simon and Owen (2001).

*Cretirhynchia* sp.; Text-fig. 5C1, 5C2, 5C3; 35 specimens from the *B. obtusa* to *B.sumensis* zones: This small biconvex brachiopod (10 mm in length) is subcircular in outline without ornament and with a uniplicate commissure. The umbo is broad and weakly curved, the beak is obtuse with a small foramen.

**Echinoids**. Echinoids are important elements in chalk faunal communities (e.g., Ernst 1970, 1972). The classification applied herein follows Kroh and Smith (2010).

**Irregular echinoids**. Apart from bivalves and brachiopods, irregular echinoids are the third-most important fossil group in the Kronsmoor section. For further reading see e.g., Ernst (1972), Schulz (1985), Jagt (2000) and Smith and Wright (2002).

*Galerites vulgaris* (Leske, 1778); Text-fig. 6D1, 6D2, 6D3; five specimens from the *B. obtusa* to *B. sumensis* zones: This small irregular echinoid (commonly 25 mm in length and width, 21 mm in height) has a high subconical corona and a subcircular outline. The peristome is rounded, the periproct rounded to pentagonal. *G. vulgaris* differs from *G. stadensis* by the non-invaginated peristome.

*Galerites stadensis* (Lambert, 1911); Text-fig. 6C1, 6C2, 6C3; eleven specimens from the *B. sumensis* Zone: This medium-sized irregular echinoid (length: 41 mm, width: 38 mm, height: 30 mm) has a low subconical corona and a subcircular outline. The peristome is well-rounded and has a small-invaginated lip. The periproct is pentagonal. There are four gonopores, and both the periproct and peristome are finely tuberculated on the oral side. *Galerites stadensis* is the only representative of the genus with an invaginated lip at the peristome margin.

*Galerites abbreviatus* (Lamarck, 1816); Text-fig. 6B1, 6B2, 6B3; 27 specimens from the *B. obtusa* to *B. sumensis* zones: This medium-sized irregular echinoid (up to 51 mm in length, 49 mm in width, 43 mm in height) has a subconical corona and a subcircular outline. The peristome is rounded to pentagonal, periproct trapezoidal to pentagonal.

*Echinocorys scutata*? Leske, 1778; Text-fig. 6A1, 6A2, 6A3; 37 specimens from the *B. obtusa* to *B. sumensis* zones: This is a large irregular echinoid with a high conical, elongated corona and ovate to subcircular outline (length: 84 mm, width: 70 mm, height: 74 mm). The peristome is oval, the periproct compressed.

**Regular echinoids**. In the Kronsmoor section, regular echinoids are less important in abundance compared to irregular echinoids (by a factor of ca. 1:2). For further reading, see e.g. Jagt (2000), Reich *et al.* (2004) and Schlüter *et al.* (2012).

*Gauthieria radiata* (Sorignet, 1850); Text-fig. 7C1, 7C2, 7C3; twelve specimens from the *B. obtusa* to *B. sumensis* zones: These small regular echinoids (22 mm in width, 10 mm in height) have an invaginated oral side and a well-rounded peristome. The bosses for spine attachment are largest on the lateral sides, decreasing in

Text-fig. 5. Brachiopods. In all figures (except Fig. B) **1**: lateral view, **2**: anterior view, **3**: dorsal view. Figs D, F and J are in natural size, all others figs × 3. **A** – *Cretirhynchia retracta* (Roemer, 1941), ShK 94. **B** – *Isocrania costata* (Sowerby, 1823), ShK 95, **B1** internal view, **B2** external view of dorsal valve. **C** – *Cretirhynchia* sp., ShK 96. **D** – *Carneithyris* sp., ShK 97. **E** – *Magas chitoniformis* (Schlotheim, 1813). ShK 98. **F** – *Carneithyris subcardinalis* (Sahni, 1925), ShK 99. **G** – *Trigonosemus pulchellus* (Nilsson, 1827), ShK 100. **H** – *Gyrosoria gracilis* (Schlotheim, 1813), ShK 101. **I** – *Terebratulina chrysalis* (Schlotheim, 1813), ShK 102. **J** – *Neoliothyrina obesa* (Sahni, 1925), ShK 103
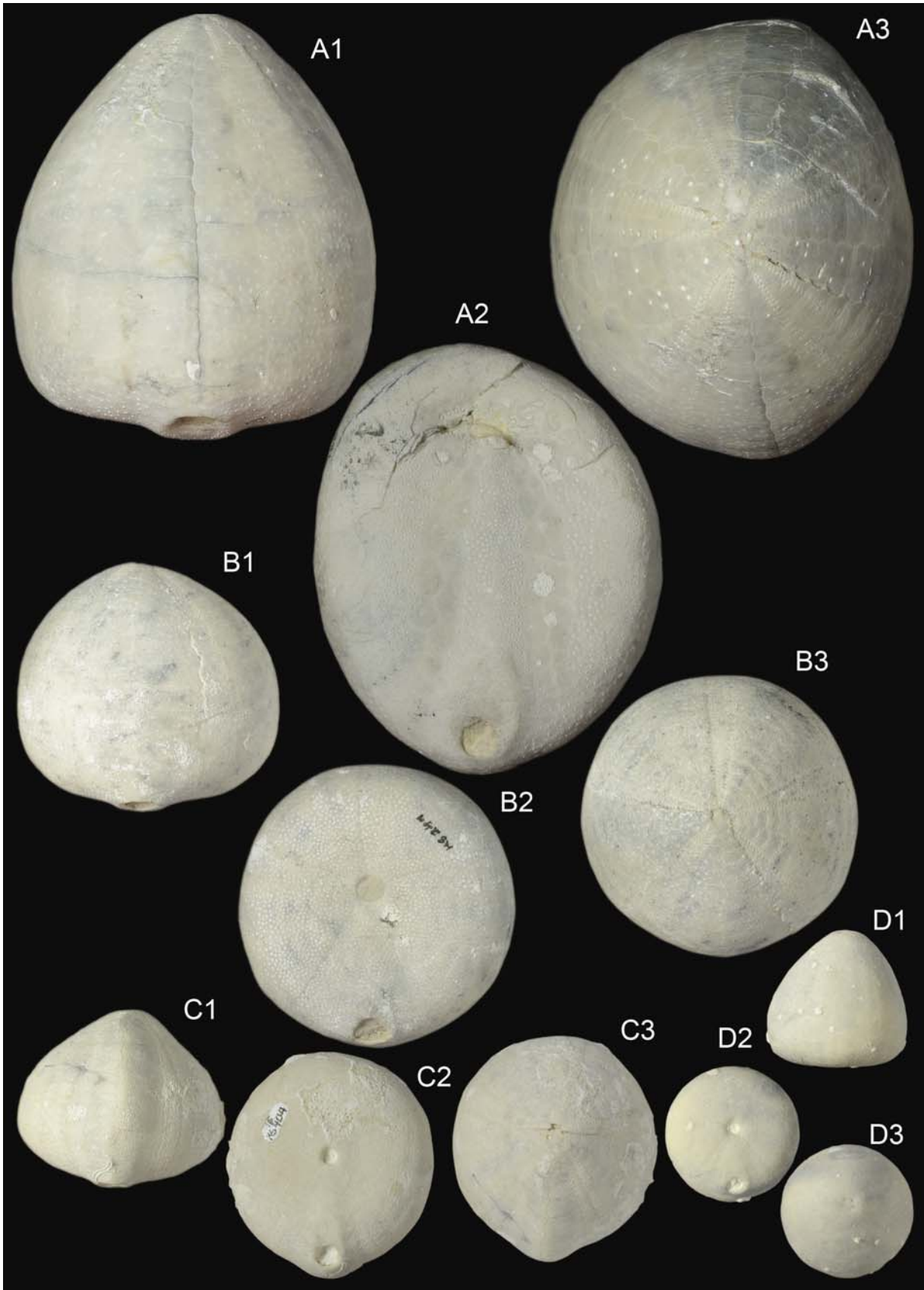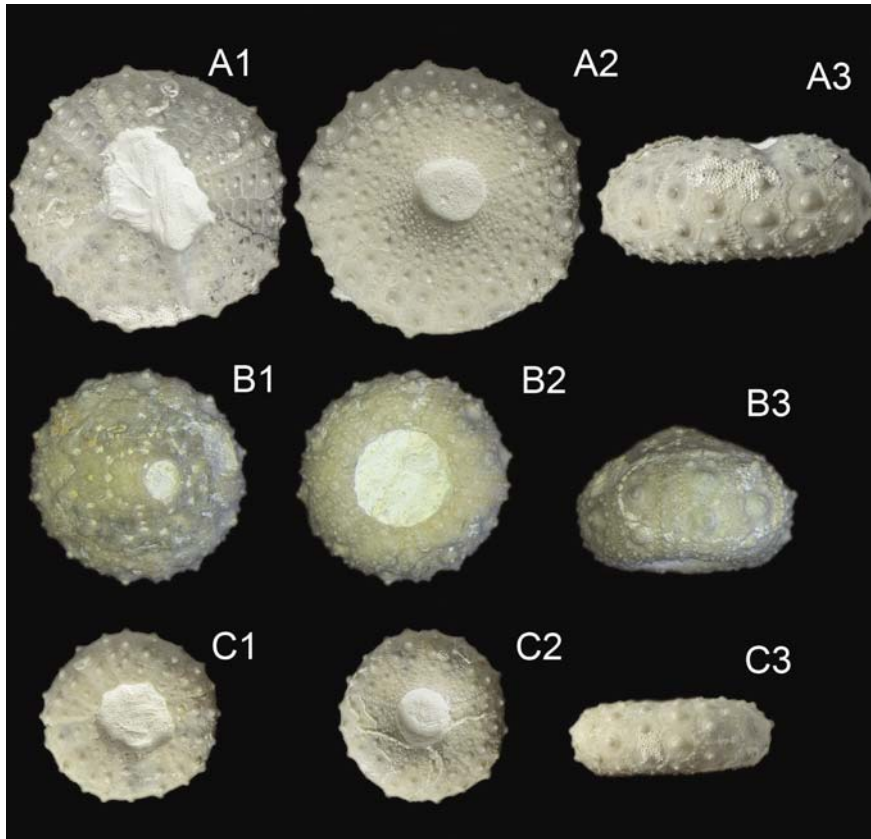
Text-fig. 7. Regular echinoids. In all figures **1**: aboral view, **2**: oral view, **3**: lateral view. **A** – *Cosmocyphus princeps* (Hagenow, 1840), ShK 80, natural size. **B** – *Salenia belgica* (Lambert, 1898), ShK 81, × 2. **C** – *Gauthieria radiata* (Sorignet, 1850), ShK 82, natural size.

size towards the oral and aboral sides. The periproct is elongate rectangular. Bryozoans and serpulids have been found on the oral and lateral sides.

*Cosmocyphus princeps* (Hagenow, 1840); Text-fig. 7A1, 7A2, 7A3; 25 specimens from the *B. obtusa* to *B. sumensis* zones: This is a small regular echinoid (corona length: 41 mm, height: 18 mm) with a flat lateral profile. The peristome is well rounded, the periproct square, the oral side invaginated. Between each pair of rows of bigger tubercles, one row of smaller tubercles is intercalated.

*Salenia belgica* (Lambert, 1898); Text-fig. 7B1, 7B2, 7B3; nine specimens from the *B. obtusa* to *B. sumensis* zones: This small regular echinoid (width: 13 mm, height: 9 mm) has a raised apical disk. The rows of primary tubercles are separated by one row of secondary tubercles and miliary granules are present. The peristome is large and rounded, the periproct is pentagonal.

**Crinoids**. Crinoids are common, however, they mainly occur as isolated columnals in washings that often cannot be safely identified. The description and identification of the crinoids follows Rasmussen (1961), Moore *et al*. (1968), Jagt (1999), Jagt and Salamon (2007) and Fearnhead (2008).

*Bourgueticrinus* sp.; Text-fig. 8E1, 8E2; four specimens from the *B. sumensis* Zone: The isolated specimen has a diameter of 4 mm with a round outline. The oval axial channel is in the centre of the smooth articular facet.

*Isselicrinus buchii* (Roemer, 1840); Text-fig. 8F, 8G1, 8G2; 17 specimens from the *B. obtusa* to *B. sumensis* zones: These straight-sided stem segments contain up to 42 columnals (diameter ca. 5 mm, total height ca. 73 mm). The external surface of the columnals is smooth, the outline pentagonal. The articular facet is crenulated following a pentalobate comarginal band of interlocked of culmina and crenellae. The lumen of the circular axial channel is narrow.

Text-fig. 6. Irregular echinoids**.** In all figures **1**: lateral view, **2**: oral view, **3**: aboral view, all in natural size. **A** – *Echinocorys scutata*? (Leske, 1778), ShK 76. **B** – *Galerites abbreviatus* (Lamarck, 1816), ShK 77. **C** – *Galerites stadensis* (Lambert, 1911), ShK 78. **D** – *Galerites vulgaris* (Leske, 1778), ShK 79

**Polychaetes**. Late Cretaceous serpulids of northern Germany were treated in detail by Jäger (1983, 1991, 2004). Gale (2002b) provided a review of serpulids known from the English Chalk and Jäger (2012) revised the serpulids from the type-Maastrichtian. We follow the taxonomy proposed by Jäger (2004).

*Nogrobs* (*Tetraditrupa*) *canteriata* (Hagenow, 1840); Text-fig. 8C1, 8C2; countless specimens in washed samples; *B. obtusa* to *B. sumensis* zones: These are coiled tubes with square cross-section, concave sides and rounded edges (~2 mm in diameter, ~20 mm in length). The edges form ridges along the tubes that are twisted. The lumen of the tubes is circular, about 1 mm in diameter.

*Pyrgopolon* sp.; Text-fig. 8D1, 8D2; countless specimens in washed samples from the *B. obtusa* to *B. sumensis* zones: The specimens are relatively large (ca. 30 mm in length, 5 mm in diameter) and only slightly coiled with a subcircular cross-section. The tubes taper weakly from the aperture to the apex, and are covered by seven ridges and faint growth lamellae. The internal lumen is large (~3 mm) in relation to diameter.

**Sponges**. Sponges are not very common in the Kronsmoor section. The skeletons of siliceous sponges most probably have been dissolved very early during diagenesis. Only three specimen of *Ventriculites*? sp. have been found, associated with a few representatives of the Calcarea. A few unidentifiable non-rigid demosponges occur in the lower part of the succession. Sponges from the chalk have received little attention and are thus poorly known. Wood (2002) provided a brief account on some common sponges of the English Chalk.

*Porosphaera globularis* (Phillips, 1829); Text-fig. 8B; 22 specimens from the *B. obtusa* to *B. sumensis* zones: The specimens are roughly spherical, ca. 9 mm in diameter. The surface shows small, more-or-less equidistant apertures (ca. 0.1–0.2 mm in diameter), one specimen is perforated (bored). The minchinellid species *P. globularis* is well known from the Upper Cretaceous of the Boreal Realm (Nestler 1961; Wood 2002; Neumann *et al*. 2008; Wilmsen *et al*. 2012; Jurkowska *et al*. 2015). Commonly, a quiet and fairly deep-water environment is inferred as the habitat of the sponges that may have been anchored to the substrate by a non-calcified dermal tissue. The perforations may represent sipunculan worm borings (Neumann *et al*. 2008).

*Ventriculites*? sp.; Text-fig. 8A; three specimens from the *B. obtusa* to *B. sumensis* zones:

These are fragmentarily preserved branching lychniscosan hexactinellids with a length of 60 mm and a minimum width of 28 mm. The dermal skeletal surface is rather smooth and densely perforated. The assignment of the specimens to the genus *Ventriculites* Mantell is doubtful based on the dermal skeletal surface structure. In *Ventriculites*, it is commonly longitudinally and/or radially ribbed, tuberculate or both, while the Kronsmoor specimens appear rather smooth.

**Corals**. The corals found in the Lower Maastrichtian of Kronsmoor are all non-hermatypic forms of the long-ranging and widely distributed genus *Parasmilia* that may also occur in deeper waters. All have originally been attached to hard substrates. For a recent overview on (Jurassic–) Cretaceous corals, see Löser (2009), Chalk corals have been discussed by Gale (2002a).

*Parasmilia excavata* (Hagenow, 1839); Text-fig. 8J1, 8J2; 41 specimens from the *B. obtusa* to *B. sumensis* zones: This is a trochoid to ceratoid solitary coral (calyx diameter 20 mm). The corallite is short and strongly curved, the calyx increases in width rapidly. The septa are partially curled, the columella is absent.

*Parasmilia centralis* (Mantell, 1822); Text-fig. 8I1, 8I2; two specimens from the *B. sumensis* Zone: This solitary coral has a curved cylindrical-conical corallite and a rounded to subcircular calyx. The calyx is up to 11 mm in diameter. Septal ridges are well-developed on the external surface of the corallite. The septa are partially curled and ornate; three orders are visible: 12 septa of first-, 12 septa of second- and 24 septa of third-order; columella present.

**Bryozoans**. Upper Cretaceous bryozoans are very rich in terms of species diversity and abundance. They have received considerable attention in the past (e.g.,Voigt 1930, 1949), but synoptic accounts and comprehensive revisions are missing. A short introduction to the most common Chalk bryozoans has been given by Taylor (2002), who, however, stated that the specific and even generic identification of the taxa is hampered by inadequate original descriptions and uncertain genus concepts. Bryozoans are fairly common in the Lower Maastrichtian of Kronsmoor, but mainly have been found as fragments in the coarse fraction of washed samples while bryozoan macrofossils are extremely rare (only three specimens). Thus, bryozoans were not considered in the present study.

**Trace fossils**. The fabric of the chalk at Kronsmoor appears rather homogenous. However, freshly cut surfaces situated stratigraphically immediately below marl seams show dense bioturbation fabrics (bioturbation index 3–4 of Droser and Bottcher 1986), but it is diffi-

cult to identify individual ichnospecies. Common ichnogenera include *Planolites* isp. and *Zoophycos* isp., and the ichnocenosis may be assigned to the *Zoophycos* ichnofacies of Seilacher (1967). A conspicuous ichnospecies, characteristic of this deeper water chalk fa-



Text-fig. 8. Miscellaneous faunal elements (sponges, crinoids, serpulids, corals, bryozoans). **A** – *Ventriculites*? sp., ShK 83, natural size. **B** – *Porosphaera globularis* (Phillips, 1829), ShK 84, × 3. **C** – *Nogrobs* (*Tetraditrupa*) *canteriata* (Hagenow, 1840), ShK 85, × 3, **C1** lateral view, **C2** aperture view. **D** – *Pyrgopolon* sp., ShK 86, × 3, **D1** aperture view, **D2** lateral view. **E** – *Bourgueticrinus* sp., ShK 87, × 3, **E1** lateral view, **E2** articular face view. **F** – *Isselicrinus buchii* (Roemer, 1840), ShK 88, natural size, lateral view. **G** – *Isselicrinus buchii* (Roemer, 1840), ShK 89, × 3, **G1** lateral view, **G2** articular face view. **H** – *Lepidenteron lewesiensis* (Mantell, 1822), ShK 91, natural size. **I** – *Parasmilia centralis* (Hagenow, 1839), ShK 92, natural size, **I1** frontal view, **I2** lateral view. **J** – *Parasmilia excavata* (Mantell, 1822), ShK 93, natural size, **J1** frontal view, **J2** lateral view
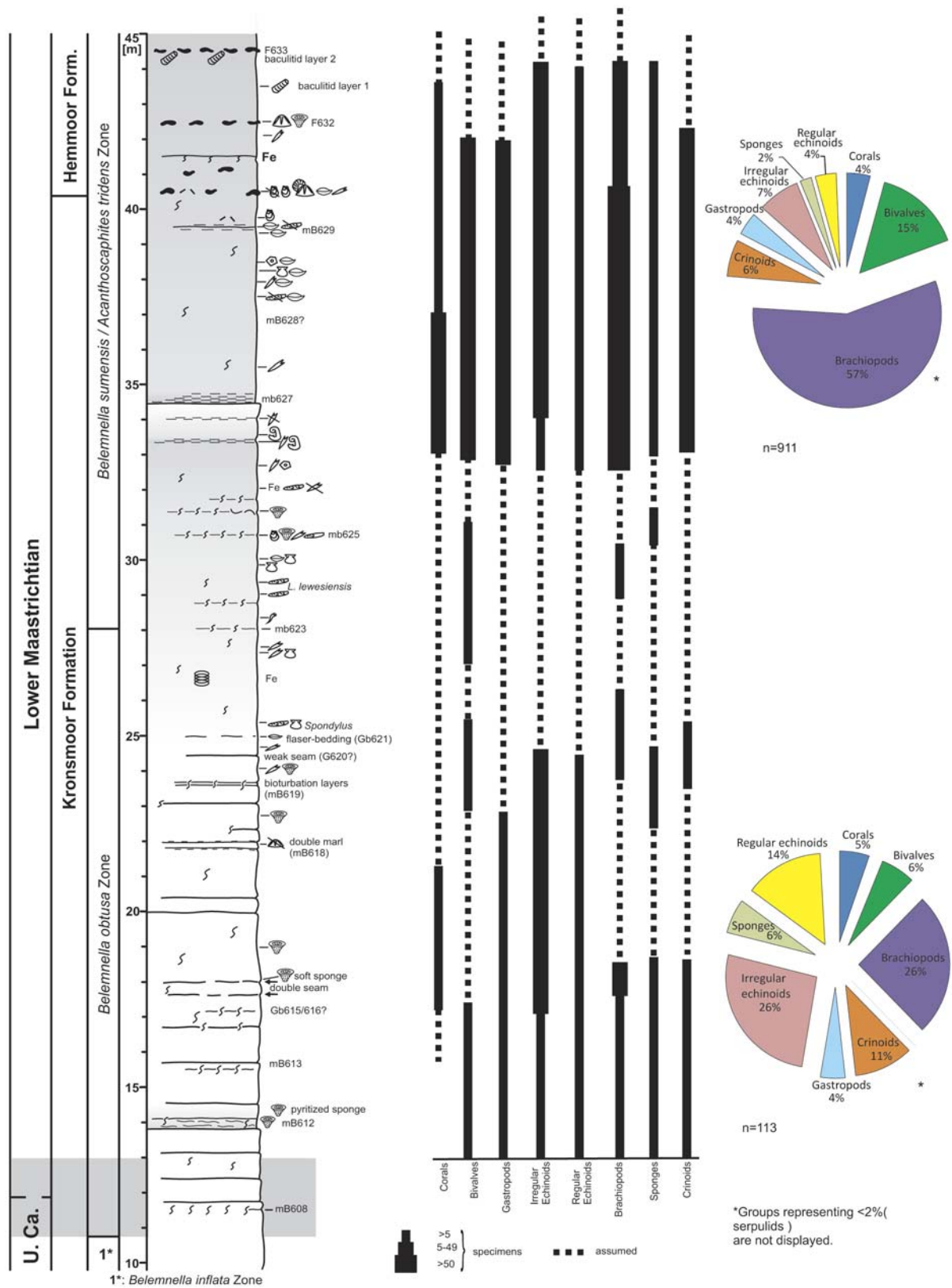
Text-fig. 9. Target interval with the abundance and stratigraphic distribution of the different principal benthic macrofossil groups in the Lower Maastrichtian *B. obtusa* and *B. sumensis* zones at Kronsmoor. For key to symbols, see Text-fig. 2

cies deposited below storm wave base, belongs to the Ichnogenus *Lepidenteron* Frič and is described below.

*Lepidenteron lewesiensis* (Mantell, 1822); Text-fig. 8H; nine specimens from the *B. obtusa* and *B. sumensis* zones: The structure consists of a tubular, unbranched accumulation of fish scales and bones, rarely of other bioclasts. It has no constructed walls. Suhr (1988) discusses different types of *Lepidenteron* and Jurkowska and Uchman (2013) described *L. lewesiensis* from Poland in detail. *L. lewesiensis* may represent indigestible feeding remains of a burrowing predator or scavenger of fishes, possibly an eunicid polychaete or an eel-like (anguillid) fish. It is common in Cretaceous deeper water marl and chalk facies deposited below storm wave base and is typical of the transition from the distal *Cruziana* to the *Zoophycos* ichnofacies (Jurkowska and Uchman 2013).

**Abundance and diversity patterns**

The study is based on more than 1,000 benthic macrofossils that have been collected largely in-situ from the Lower Maastrichtian of the Kronsmoor section. The fossils have been accumulated over two decades of collections independently of their taxonomic affinity, and of their state of preservation, under comparable outcrop conditions from the entire range of the section. A collection bias towards better preserved and/or preferred

taxa is therefore implausible, albeit the fossils have not been retrieved by truly standardized sampling methods (e.g. Gale *et al*. 2000). Nonetheless, some fundamental differences can be recognized in the benthic macroinvertebrate assemblages between the lower part (upper part of the Kronsmoor Formation, *B. obtusa* Zone, ca. 16 m in thickness) and the upper part of the section (uppermost Kronsmoor and lowermost Hemmoor formations, lower to middle *B. sumensis* Zone, ca. 15 m in thickness). This two-fold subdivision of the studied succession is supported by quantitative studies of the meso- and microfossil contents which are currently underway. Furthermore, nektic macroinvertebrates show conspicuous abundance and diversity shifts in the Lower Maastrichtian of Kronsmoor (Schulz 1979; Niebuhr 2003; Wilmsen and Esser 2004; Niebuhr *et al*. 2011).

The lower interval (*B. obtusa* Zone) is poorly fossiliferous and only 113 benthic macrofossil specimens were collected, mostly irregular echinoids, brachiopods, regular echinoids and crinoids (Text-fig. 9, Table 1). The upper interval (lower to middle *B. sumensis* Zone) yielded 911 benthic macrofossil specimens with an overall much higher diversity (Table 1). Considering the nearly equal thicknesses and accessibilities of the two parts, this is a significant difference.

Concerning the absolute abundance, the principal macrofossil groups always have higher abundances in the upper interval (Table 1). As an example, there is a general increase of brachiopods from only 29 specimens

| Groups | Lower interval (*B. obtusa*) | | | Upper interval (*B. sumensis* Zone) | | |
|---|---|---|---|---|---|---|
| | A bundance | Genera | Species | A bundance | Genera | Species |
| **Corals** | 6 | 1 | 1 | 37 | 1 | 2 |
| **Bivalves** | 7 | 3 | 3 | 138 | 9 | 11 |
| **Brachiopods** | 29 | 6 | 7 | 519 | 9 | 11 |
| **Crinoids** | 12 | 2 | 2 | 58 | 3 | 3 |
| **Gastropods** | 5 | 4? | 4 | 36 | 6? | 6 |
| **Irregular echinoids** | 30 | 3 | 4 | 66 | 3 | 7 |
| **Regular echinoids** | 16 | 4 | 4 | 33 | 4 | 4 |
| **Serpulids*** | 1 | 1 | 1 | 6 | 3 | 3 |
| **Sponges** | 7 | 2 | 2 | 18 | 2 | 2 |
| **total** | 113 | 22 | 28(2) | 911 | 35 | 49(23) |

Table 1. Generic and specific abundances of the different principal benthic macrofossil groups in the Lower Maastrichtian of Kronsmoor. In parenthesizes: species that occur only in the lower or upper interval. *More specimens and species exist in washed samples in both zones. Gastropods: question mark in genera column denotes the taxonomic problems outlined in the systematic chapter above; the number under species represents different morphotypes

in the lower interval to over 500 specimens in the upper interval. Even more spectacular is the increase in abundance of the brachiopod genera *Carneithyris*, *Cretirhynchia* and *Magas*: only a few specimens of each genus have been collected from the lower interval, while in the upper interval their abundances increased to 120–157 specimens per genus. Also bivalves significantly increase in abundance, from only seven specimens in the *B. obtusa* Zone to 137 specimens in the upper interval. The two common Cretaceous bivalve genera, *Pycnodonte* and *Spondylus*, rise from only a few specimens in the *B. obtusa* Zone to up to 20 to 50 specimens, respectively, in the upper interval. In most of the other groups, the increase is less spectacular but never less than 1:2 (Table 1).

A similar, although not so spectacular, pattern is seen in the generic and specific diversity plots (Table 1): those from the lower interval (22/28) are conspicuously lower than those in the upper interval (35/49). In most of the groups, this 1:2 diversity increase is, however, much smaller than the massive abundance increase (1:8) between the intervals studied. In some groups this difference is still more conspicuous, as e.g., in brachiopods, in which the 1:18 abundance increase corresponds to only 1:1.5 species and genus diversity in-

crease. A distinctly higher than average diversity increase is noted in bivalves; a triple increase in species and almost fourfold increase in the genus diversity (Table 1). Genera which are only present in the upper interval are *Entolium*, *Hyotissa*, *Limatula*, *Neithea, and Lyropecten*. It is interesting to note that just two species only occur in the lower interval while 23 species are restricted to upper interval (species richness 28/49).

DISCUSSION

**Palaeoecology**

In the palaeoecological analysis the feeding and living modes of the benthic macrofauna are considered. For this purpose, the taxa were assigned to guilds. Guilds are groups of species that are not necessarily taxonomically closely related (i.e., polyphyletic) but that have similar ecological resource requirements and nutrition strategies and, thus, occupy similar roles in faunal communities. Guild classifications include the life site, the habitat, the mode of feeding and morphological adaptations of the organism (see Bambach 1983; Aberhan 1994; Brenchley and Harper 1998). The purpose of guild analy-
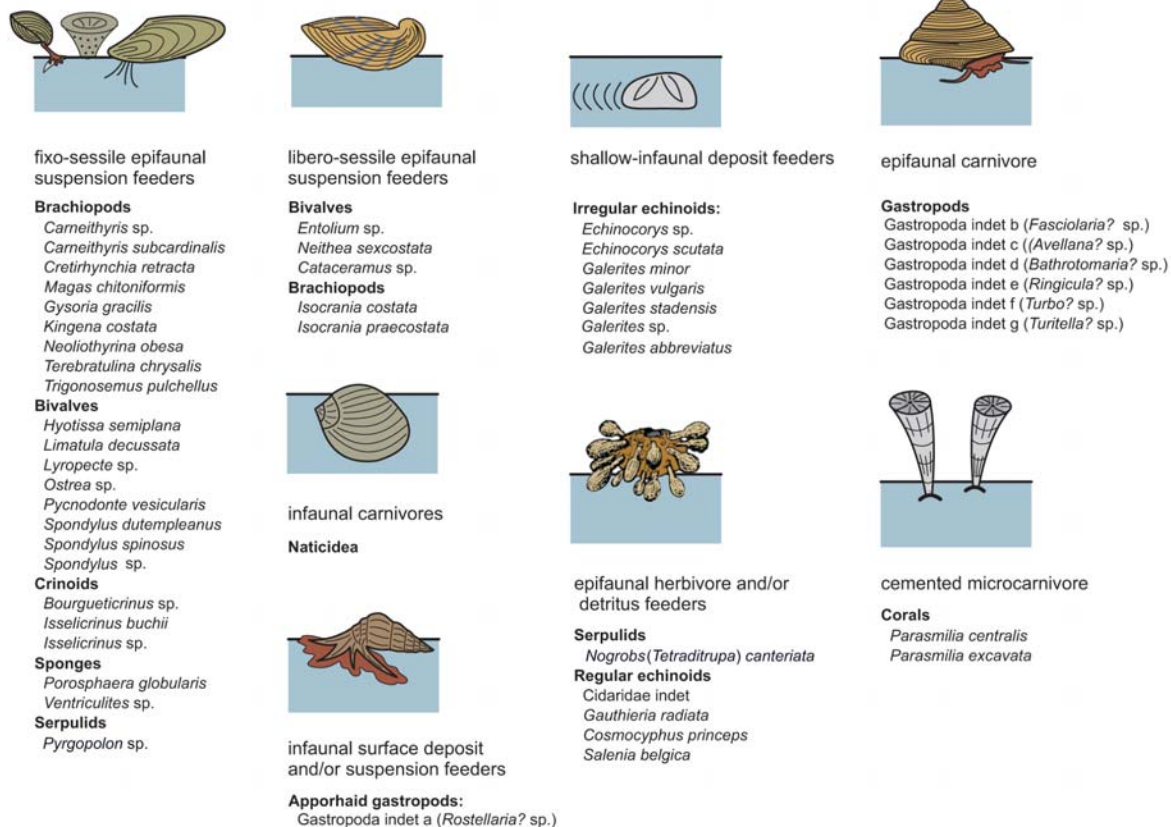


Text-fig. 10. Macrobenthic guilds identified in the Lower Maastrichtian of Kronsmoor with allocated taxa (guild structure modified after e.g., Aberhan 1994; Lauridsen and Surlyk 2008; Hansen and Surlyk 2014)

sis is to examine the habitat structure of a community as it functions in a certain place at a certain time. The guild assignments proposed herein (Text-fig. 10) are based on available autecological literature and databases (e.g., Paleobiology database: fossilworks.org), on the interpretation of functional morphologies, and/or on comparison with closely related extant relatives (Ager 1965; Carter 1968, 1972; Ernst 1970; Rudwick 1970; Stanley 1970; Surlyk 1972; Thayer 1975; La Barbera 1981; Abdel-Gawad 1986; Aberhan 1994; Fürsich and Hurst 1994; Machalski and Robaszewska 2003; Wilmsen *et al*. 2007; Lauridsen and Surlyk 2008; Lauridsen *et al*. 2009; Hansen and Surlyk 2014).

In order not to split the fauna into too many guilds, we combined the epibyssate, cemented and pedunculate epifaunal suspension feeder guilds that have been separated by Aberhan (1994) into the fixo-sessile epifaunal suspension feeder guild. This guild merging respects the life site, the habitat and the mode of feeding of the organism, and only disregards the negligible different morphological adaptations to achieve stable fixation to the sea floor. In total, eight guilds were identified in this study.

Guild 1: Fixo-sessile epifaunal suspension feeders: most of the bivalves recorded from the Lower Maastrichtian of Kronsmoor can be classified to this guild (Text-fig. 10). It includes also sponges, crinoids, serpulids and pedunculate brachiopods (note that some taxa may be secondarily free-lying as adults).

Guild 2: Libero-sessile epifaunal suspension feeders: this guild includes some bivalves and brachiopods.

Guild 3: Infaunal carnivores: the infaunal carnivores are only indirectly proven by the presence of characteristic boreholes in the shells of e.g. brachiopods.

Guild 4: Infaunal surface deposit and/or suspension feeders: this group is very rare and may only be represented by a few apporhaid gastropods.

Guild 5: Shallow-infaunal deposit feeders: all irregular echinoids belong to this group albeit some taxa (i.e., *Galerites*) may have lived epifaunally and were grazer-deposit feeders.

Guild 6: Epifaunal herbivore and/or detritus feeders: all regular echinoids are grouped in this guild.

Guild 7: Epifaunal carnivores: this guild groups some gastropods.

Guild 8: Cemented microcarnivores: this guild is represented by solitary corals.

The trophic nuclei, comprising the numerically most important elements that make up 80% of the fauna (Aberhan 1994), of the lower and upper interval, are quite different (Text-fig. 11). The most significant change is the dominance of the fixo-sessile epifaunal suspension feeder guild from 46% in the lower interval to 66% in the upper interval. Likewise, there is also a significant increase of the libero-sessile epifaunal suspension feeders (7% in the lower interval, 20% in the upper interval). Shallow infaunal deposits feeders, on the other hand, are more important in the upper interval (30% versus 6%). The epifaunal suspension feeders, comprising only 53% of the trophic nucleus of the lower interval, are of overwhelming importance in the upper interval (86%).
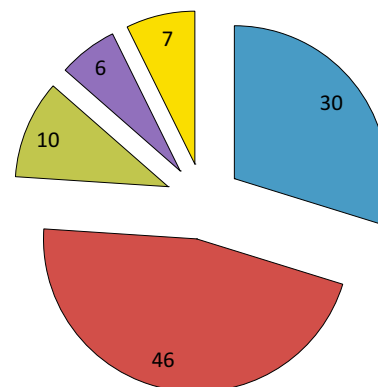
**Palaeoenvironment**

The main physico-chemical environmental factors influencing deposition during the Early Maastrichtian at Kronsmoor can be evaluated based on a number of sedimentary and biofacies indicators. Biological factors such as predation, however, are much more difficult to reconstruct and are not considered in the following discussion.
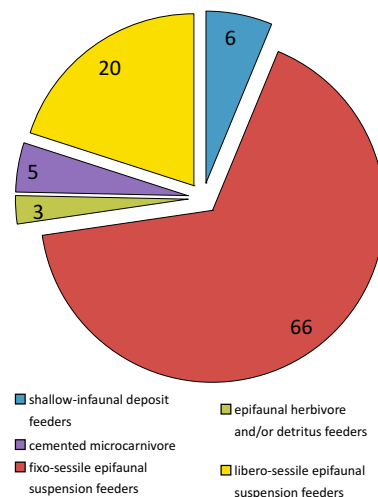


Text-fig. 11. Trophic nuclei of the Lower Maastrichtian *B. obtusa* and *B. sumensis* zones at Kronsmoor

The continuous abundance of stenohaline organisms (e.g., echinoids, crinoids, brachiopods) indicates normal marine salinity throughout the studied interval. The distance to continental areas with potential fluvial input is in the order of several hundred kilometres (Text-fig. 1) and makes freshwater effects highly unlikely. The sedimentary fabric (fine-grained chalk) indicates deposition in a calm offshore environment below storm-wave base with a soft-bottom substrate (e.g., Ineson *et al.* 2005). The absence of any photic elements (e.g., hermatypic corals, calcareous algae) suggests the situation of the sea floor below the euphotic zone (see compilation in Luterbacher 1984). Pervasive bioturbation, the lack of black shales and laminations indicate normal oxygenation of the water column and the upper part of the sediment layer (e.g., Oschmann 1991).

All identified bivalves lived epifaunally although many Mesozoic bivalves had an infaunal lifestyle (Stanley 1970; Aberhan 1994). In the absence of any indications for oxygen depletion, a possible explanation could be the secondary, diagenetic removal of their aragonite shells (Voigt 1996; Wright *et al*. 2003). Infaunally living bivalves often had aragonite shells that were commonly dissolved in the chalk, except in hardground environments (Heinberg 1999). This process may also explain the low abundance of gastropods. Thus, a taphonomic bias on our results cannot be excluded. A potential dissolution of aragonite shells does not, however, explain why the upper part of the section is much more fossiliferous than the lower one.

Nutrients are very important for benthic communities (Graf 1992). The benthic macrofossil assemblages of Kronsmoor consist mostly of epifaunal suspension feeders and shallow-infaunal deposit feeders that were dependent on the availability of particulate organic matter (53% and 30% in the lower interval versus 86% and 6% in the upper interval). According to Aberhan (1994), Late Cretaceous fine-grained chalk mid- to outer-shelf environments show a high percentage of epifaunal free-lying suspension feeders while pedunculate brachiopods are rare. Our results indicate that the fixo-sessile epifaunal suspension feeders were dominant, including a considerable number of rhynchonelliform brachiopods, especially in the upper interval. This stenotopic group is dependent on stable, normal marine oxygen availability and salinity, as well as low to moderate sedimentation rates, and is thus uncommon in physically stressed environments (e.g., Rudwick 1970). Their relative importance constantly decreased during the Mesozoic due to the adaptive superiority of bivalves (Gould and Calloway 1980; Aberhan 1994). At the moment it can only be speculated what factor triggered the abundance peak of brachiopods (and other fauna) in the upper interval. It is tempting to relate this shift to changes in nutrient sup-

ply and/or water depth. Hansen and Surlyk (2014), for example, related the poorly diverse and less dense level-bottom community of the upper Sigerslev Member in the uppermost Maastrichtian of the Danish Basin to deeper water and low-nutrient conditions, in contrast to the more diverse and abundant under- and overlying communities assigned to shallower and more nutrient-rich conditions. Such distribution patterns of benthic macrofauna in relation to water depth and nutrient supply can also be observed in recent shelf settings (Probert and Anderson 1986). In the same way, the low-diversity and low-abundance lower interval assemblage may be interpreted as a oligotrophic deeper water setting while the high-diversity and abundance upper interval assemblage may reflect nutrient-rich and slightly shallower conditions (the up-section slightly increasing clay content may indicate a weak shallowing trend). On the other hand, under some circumstances such as low-food and low-oxygen availability, brachiopods may be superior to bivalves, and they may also use dissolved organic matter for nutrition (Rudwick 1970; Gould and Calloway 1980; Tunnicliffe and Wilson 1988). The brachiopod bloom in the upper interval (*B. sumensis* Zone) at Kronsmoor may thus also be interpreted in terms of a decrease in the availability of particulate food. Interestingly, Schönfeld (1990) interpreted a maximum in accumulation rates of planktic foraminifera and fish remains in the *B. obtusa* Zone as an indication of high primary productivity, with only a subordinate peak in the *B. sumensis* Zone, just below the base of the Hemmoor Formation. Furthermore, Linnert *et al.* (2016) suggested, based on high-resolution calcareous nannofossil data, that the Early Maastrichtian nutrient regime shifted from nitrate-limited in the lower part to phosphate-limited in the upper part of the succession. In summary, the story may be more complex than anticipated.

**Nektic macroinvertebrates**

Nektic macroinvertebrates show conspicuous abundance and diversity shifts in the Lower Maastrichtian of Kronsmoor. Above a gap in the belemnite record across the Campanian–Maastrichtian boundary interval (between mB608-2m to mB608; Niebuhr *et al*. 2011), representatives of the genus *Belemnella* (see Remin 2012 for a recent taxonomic revision) are moderately common in the *B. obtusa* Zone (57 specimens). In the *B. sumensis* Zone, *Belemnella* starts to get more common in marl layer mB625, reaching an abundance peak between marl layer mB626 and flint layer F630 in the mid-*B. sumensis* Zone (107 specimens). Ammonites are rare and poorly diverse in the *B. obtusa* and lower *B. sumensis* zones, being much more common and diverse in the up-

permost Kronsmoor and lowermost Hemmoor formations (mid-*B. sumensis* Zone) between marl layer mB626 and flint layer F633 (Niebuhr 2003). Noteworthy are flood abundances of the ammonite *Acanthoscaphites tridens* in marl layer mB626 and two baculitid layers in the lowermost Hemmoor Formation. Furthermore, nautilids, albeit only known by two species, have an abundance maximum in the *B. sumensis* Zone with a peak between mB627 and F631 (Wilmsen and Esser 2004).

CONCLUSION

Two successive benthic macrofossil assemblages have been recognised in the Lower Maastrichtian chalk of Kronsmoor. The lower interval corresponds to the upper part of the Kronsmoor Formation (*B. obtusa* Zone, ca. 16 m thick) and the upper interval comprises the uppermost Kronsmoor and lowermost Hemmoor formations (lower to middle *B. sumensis* Zone, ca. 15 m thick). The assemblage of the lower interval is characterized by low abundances. The assemblage of the upper interval, on the other hand, shows an eight-times higher abundance of macroinvertebrates and a conspicuous dominance of brachiopods. Also the generic/specific diversity increases, but much lower than the abundance (22/28 and 35/49 for the lower and upper parts, respectively). Palaeoecological analysis indicates the presence of eight different guilds that combine systematically diverse organisms of similar life site, habitat, and mode of feeding. Epifaunal suspension feeders (fixo-sessile and libero-sessile guilds), comprising approximately half of the trophic nucleus of the lower interval, increased to a dominance of 86% in the upper interval. It is tempting to relate this shift from the lower to the upper interval to changes in nutrient supply and/or water depth (i.e. an increase in nutrient availability and shallowing of the depositional environment). However, the dominance of brachiopods is peculiar and thus, further meso-, micro-, nannopalaeontological data as well as geochemical proxies are needed to explain the macrofossil distribution patterns in the Lower Maastrichtian of Kronsmoor.

**Acknowledgements**

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