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Early representatives of the belemnite genus *Belemnella* (Cephalopoda) from the uppermost Campanian–Lower Maastrichtian of the Middle Vistula River section, central Poland

NORBERT KEUTGEN[1], ZBIGNIEW REMIN[2] AND IRENEUSZ WALASZCZYK[2]

[1] *ZFiPBR, Uniwersytet Techniczno-Przyrodniczy Bydgoszcz, ul. Bernardynska 6/8, PL-85-029 Bydgoszcz, Poland.*
E-mail: keutgen@utp.edu.pl
[2] *Faculty of Geology, University of Warsaw, Al. Żwirki i Wigury 93, PL-02-089 Warsaw, Poland.*
E-mails: zbyh@uw.edu.pl, i.walaszczyk@uw.edu.pl

ABSTRACT:

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Representatives of the belemnite genus *Belemnella* from the uppermost Campanian and lowermost Maastrichtian of the Middle Vistula River Valley section (central Poland) have been studied, using the species concept proposed by Schulz in 1979. Results have been compared to a recently proposed new interpretation of the genus *Belemnella* based on artificial neural networks, as put forward by Remin in 2007 and 2012. In the interval studied, four taxa have been recognised: *Bln. longissima*, *Bln. inflata*, *Bln. obtusa* and *Bln. vistulensis*, the last-named being a senior synonym of *Bln. pseudobtusa*. Three additional forms have been left in open nomenclature: *Bln*. cf. *lanceolata*, *Bln*. ex gr. *lanceolata/inflata* and *Belemnella* sp. Based on their documented vertical ranges, three *Belemnella* standard zones, as originally distinguished in the Kronsmoor section by Schulz (1979), northern Germany, have been defined, in ascending order: the *Bln. lanceolata*, *Bln. vistulensis* and *Bln. obtusa* zones. The bases of the *lanceolata* and *obtusa* zones in the Middle Vistula River Valley section can be directly correlated with the same zones at Kronsmoor, and appear to be isochronous within limits of stratigraphic resolution. The base of the *vistulensis* Zone (*Bln. vistulensis* according to the species concept of Schulz in 1979), however, is probably diachronous, being older in the Middle Vistula section. Although Schulz's and Remin's species concepts differ quite considerably, they do result in similar stratigraphic subdivisions of the Kronsmoor and Middle Vistula River sections.

Key words: *Belemnella*; Biostratigraphy; Species concepts; Middle Vistula River section; Campanian–Maastrichtian boundary.

INTRODUCTION

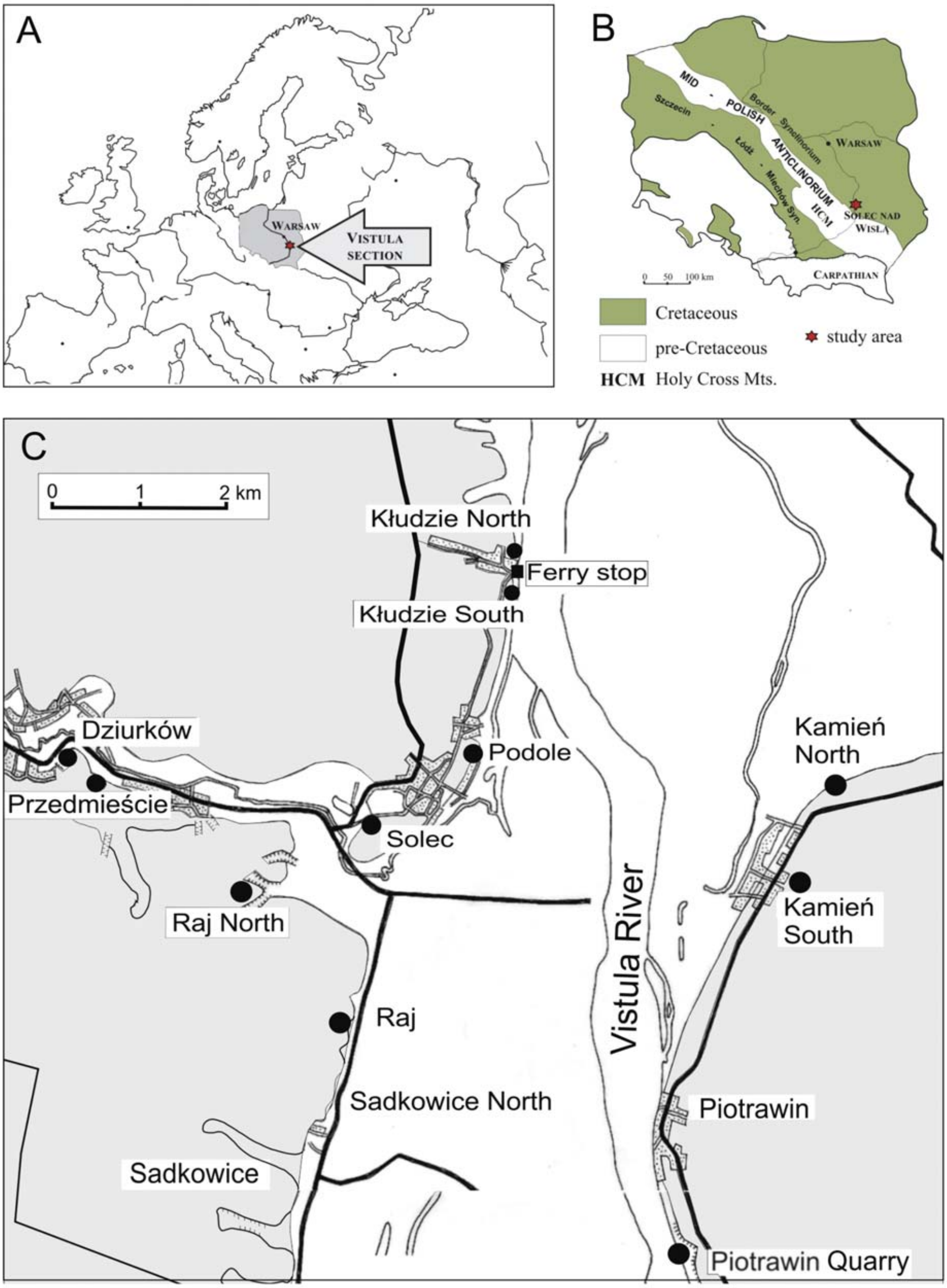
The Middle Vistula River section (Text-fig. 1A) represents one of the most complete sequences in Europe exposing the Campanian–Maastrichtian boundary succession (Pożaryski 1938; Błaszkiewicz 1980; Walaszczyk 2004). In addition, all of the stratigraphically important macro- and microfossils are both common and well preserved. Hence, this section may represent one of the few, if not the sole, that allows firm correlations between the belemnite zones of the Central European and Central Russian Subprovinces (North European palaeobiogeographic Province) with the Tethyan Realm, where the Global Standard Stratotype Section and Point for the Campanian–Maastrichtian boundary has been established.

To a large extent, the biostratigraphy of Upper Campanian and Maastrichtian strata in Central Europe and Central Russia is based on belemnites. Originally, the Campanian–Maastrichtian boundary was defined by the FAD of *Belemnella lanceolata* (von Schlotheim, 1813) in the Boreal Realm (Schulz *et al*. 1984). However, at the Symposium on Cretaceous Stage Boundaries in Brussels (1995), the section at Tercis les Bains (near Dax, Landes; southwest France) in the Tethyan Realm was proposed as the Global Standard Stratotype Section and Point (GSSP) for the Campanian–Maastrichtian boundary (Odin 1996); this was later ratified (Odin and Lamaurelle 2001). In view of the fact that belemnites do not occur at Tercis, the correlation of the GSSP for the Campanian–Maastrichtian boundary with Boreal sections has long been a matter of debate. A recent multistratigraphic analysis (Niebuhr *et al*. 2011) has proposed correlation of the boundary as defined at Tercis with a level c. 11 m above flint layer F 600 at the „Saturn“ quarry (Kronsmoor, northern Germany). As previously proposed by Christensen *et al*. (2000), this level roughly matches the FAD of *Belemnella vistulensis* (Kongiel, 1962), of which *Bln. pseudobtusa* Schulz, 1979, is a junior synonym.

Remin (2007, 2008, 2012) reinvestigated *Belemnella* samples from the Kronsmoor section, in addition to specimens from the Middle Vistula River Valley section using an alternative systematic approach. He developed a new species concept by applying artificial neural networks (AANs), in particular the self-organising Kohonen networks. This approach was aimed at maximum objectification in the taxonomic study of belemnites. Some of the previous studies, notably those by W.K. Christensen and M.-G. Schulz, started with the hypothesis that but a single belemnite species is present in a sample from a particular time interval at a single locality. This hypothesis was either accepted or rejected after testing the measured values of parameters studied for normal distribution and variance homogeneity. In subsequent analyses, also the coefficient of variation was included in evaluation of the hypothesis. The comparison of such a population (or sample in those cases where more than one species was present) with additional samples from different stratigraphic levels at the same locality was used in order to identify an evolutionary lineage and within this lineage the range of variation. Individual specimens that did not fit this range of variation and were missing in the stratigraphically older and/or younger sample(s) were considered to belong to another (or other) species. Comparison of additional species thus identified with populations from different, albeit coeval, localities led to their adequate identification. Hence, a certain step in the approach used by Christensen and Schulz is characterised by an – although based on objective considerations – *a priori* subdivision of the belemnite guards into distinct groups prior to calculation of population statistical parameters such as mean values and standard deviation.

These approaches (Schulz 1979; Remin 2007, 2008, 2012) resulted in different species concepts within the genus *Belemnella*. For instance, *Belemnella lanceolata* (von Schlotheim, 1813) *sensu* Remin (2012) includes specimens that were previously classified by Schulz (1979) as *Bln*. (*Bln*.) *lanceolata*, *Bln*. (*Bln*.) *longissima*, *Bln*. (*P.*) *desnensis* and most specimens were covered by his wide concept of *Belemnella* (*P*.) *inflata*, while *Belemnella vistulensis* of Remin (2012) (*Belemnella* sp. I in Niebuhr *et al*. 2011, p. 203) includes representatives of three species, assigned previously by Schulz (1979) to *Bln*. (*P*.) *inflata*, *Bln*. (*P*.) *pseudobtusa* and *Bln*. (*P*.) *obtusa*. In summary, Remin's species cannot be seen as a further development of the concepts proposed by Christensen and Schulz, but must be viewed as an independent approach which leads to different taxonomic results. Hence, the present authors consider it important, at least for the time being, to apply both species concepts in parallel. If both prove to be applicable, they should at least result in similar conclusions with respect to stratigraphic correlation. Further studies are needed to improve, and possibly merge, both approaches. The aim of the present study is therefore to identify representatives of *Belemnella* from the Middle Vistula River Valley section, collected and described by Remin (2012), by using Schulz's method (1979).

In addition, the documented ranges of early species of *Belemnella* from the Kronsmoor section are here compared with temperature data presented by Niebuhr *et al*. (2011). These data are used to account for the punctuated appearance of belemnite species and, in part, for dramatic changes in species assemblages of the genus *Belemnella* Nowak, 1913 within the Campanian–Maastrichtian boundary interval. Moreover, these temperature changes might explain the gradual replacement of representatives of the genus *Belemnitella* d'Orbigny, 1840 by *Belemnella* during the latest Campanian.



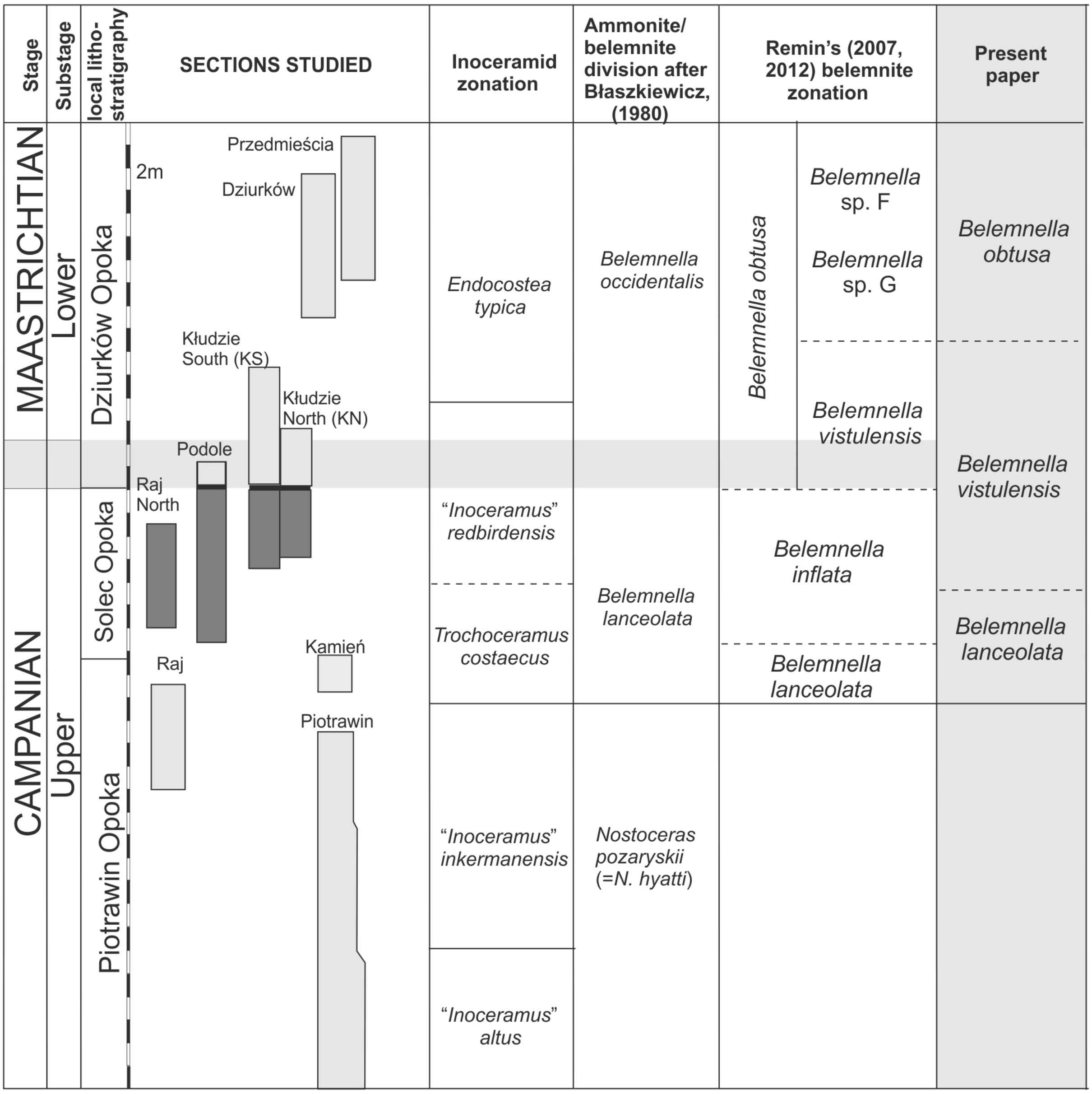
Text-fig. 1. A) location of the Middle Vistula River Valley and Kronsmoor sections in Europe; B) Upper Cretaceous deposits in extra-Carpathian Poland, and C) location of uppermost Campanian and lowermost Maastrichtian localities of the Middle Vistula River Valley section, mentioned in the text; A-B – after Remin (2012); C – after Walaszczyk (2012)

GEOLOGICAL SETTING AND LIST OF LOCALITIES

The Campanian–Maastrichtian boundary succession in the Middle Vistula River Valley section (Text-fig. 1B) is comparatively monotonous, representing the opoka facies. From the base to top the Piotrawin, Solec and Dziurków opoka units have been distinguished (Walaszczyk 2004; Text-fig. 2). While Piotrawin and Dziurków are characterised as pure opoka, the Solec Opoka represents a marly variety.

The source localities of the belemnites studied (Text-figs. 2) are shortly characterised below, together with species of *Belemnella* recognised by employing Schulz's (1979) concept As the same material is described by Remin (2012, this issue), the reader is referred to that paper for a more detailed description of the localities (see also Walaszczyk 2004, and 2012, this issue).

Raj: Small quarry exposing c. 7 m of pure, light-yellow, fossiliferous opoka, referred to the topmost part



Text-fig. 2. Belemnite zonation of the uppermost Campanian and lowermost Maastrichtian succession of the Middle Vistula River Valley section and comparison with Remin's (2007, 2012) belemnite zonation; chronostratigraphic location of Middle Vistula River Valley localities and its inoceramid zonation after Walaszczyk (2004); ammonite zonation after Błaszkiewicz (1980; with comments in Walaszczyk 2004) of the Piotrawin Opoka (Walaszczyk 2004). The highest levels at this quarry yielded the oldest representatives of the genus *Belemnella*, here referred to *Belemnella* sp. It is concluded that the uppermost part of the Piotrawin Opoka exposed at the Raj quarry belongs already to the *lanceolata* Zone *sensu* Schulz (1979).

Raj N: Small quarry, southwest of the town of Solec, exposing 9 m of grey, relatively hard, marly opoka, already belonging to the Solec Opoka. As far as belemnites are concerned, species richness here has markedly increased in comparison to the Raj quarry. Four species of *Belemnella* have been documented: *Bln.* cf. *lanceolata*, *Bln*. *longissima*, *Bln*. *inflata* and *Bln. vistulensis*. The presence of *Bln. vistulensis*, a senior synonym of *Bln. pseudobtusa* (index of the *pseudobtusa* Zone at Kronsmoor), indicates that its base is situated within this section. The precise entry level of *Bln. vistulensis* is, however, not yet known; additional, well-horizoned material is needed.

Worth of note is that the Raj N section also yielded three clavate forms of *Bln. inflata* which resemble *Bln. desnensis* (Jeletzky, 1941) *sensu* Schulz (1979). Such forms have not been observed in material from the stratigraphically younger Kłudzie N section. Thus, they might hint at the presence of equivalents of the middle *lanceolata* Zone *sensu germanico* within the Raj N section.

Podole: The Podole section exposes about 16 m of Solec Opoka, the ‘boundary marl’, almost at its top, and the basal part (c. 1 m) of the Dziurków Opoka at its top. Two belemnites were collected from the Solec Opoka and five from the Dziurków Opoka, all belonging to *Bln. vistulensis*.

Kłudzie S: About 100 m south of the Kłudzie Ferry stop, 18 m of opoka are exposed with the ‘boundary marl’ separating the Solec and Dziurów opokas in the middle part of the succession. Three complete rostra of *Belemnella* are available, all referred here to *Bln. vistulensis*.

Kłudzie N: About 6 m of opoka is exposed in the left bank of the Vistula River, north of the Kłudzie Ferry stop. The so-called ‘boundary marl’, a 20–30 cm thick marly horizon, is found c. 6 m above the Vistula River level (Walaszczyk 2004). At some distance above the ‘boundary marl’ occurs the gradual lithological change between the Solec and Dziurków opokas.

Belemnites from Kłudzie N are all from the Solec Opoka below the ‘boundary marl’. Although the material is limited, three species could be determined: *Bln.* cf. *lanceolata* (1 specimen), *Bln*. *inflata* (3) and *Bln. vistulensis* (1). The presence of the last-named species indicates the *vistulensis* Zone.

Dziurków: The 12 m thick succession of the Dziurków Opoka yielded two species of *Belemnella*. The majority of specimens represent *Bln*. *obtusa* (7 specimens), while two rostra are referred to *Bln*. ex gr. *lanceolata*/*inflata*. The mean values of the population of *Bln. obtusa* indicate early forms, which favour correlation with the lower c. 3 m of the *obtusa* Zone at Kronsmoor.

BELEMNITE ZONES OF SCHULZ IN THE MIDDLE VISTULA RIVER VALLEY SECTION AND A COMPARISON WITH KRONSMOOR

Based on Schulz’s (1979) concept, three zones of *Belemnella* can be identified in the uppermost Campanian and Lower Maastrichtian strata of the Vistula River Valley exposed between the sections of Raj and Dziurków: the *lanceolata, vistulensis* (= *pseudobtusa* of Schulz, 1979) and *obtusa* zones.

The first representatives of the genus *Belemnella*, i.e. one specimen and an alveolar fragment with a portion of the rostrum solidum, originate from the uppermost part of the Piotrawin Opoka at Raj. Remin (2012) referred these specimens to *Bln. lanceolata*; here, they are listed as *Belemnella* sp., because the limited number of specimens does not allow a specific determination. They belong either to *Bln*. *lanceolata* or *Bln. inflata* (Arkhangelsky, 1912), as understood by Schulz (1979). Both species might be present within the lowermost 3 m of the *lanceolata* Zone at Kronsmoor (Schulz 1979).

The base of the *vistulensis* Zone (*pseudobtusa* Zone, *sensu* Schulz, 1979) is situated in the Solec Opoka at the Raj N quarry. Its exact position is unknown, but it should be approximately 7 to 13 m (according to Walaszczyk 2004) above the base of the *lanceolata* Zone.

The precise level of the upper boundary of the *vistulensis* Zone has not been identified, but this undoubtedly is situated within the Dziurków Opoka. The fact that the Dziurków quarry has produced rather primitive forms of *Bln. obtusa* Schulz, 1979, implies that the top of the *vistulensis* Zone must occur close to the quarry floor or even within its lowermost part. The base of the Dziurków section is situated about 35 m above the base of the *lanceolata* Zone (see Walaszczyk 2004). Hence, 35 m in the Middle Vistula River Valley section would correspond to 15 m in the Kronsmoor section, implying a higher sedimentation rate for the Vistula section. For the *vistulensis* Zone (*pseudobtusa* Zone of Schulz 1979) at Kronsmoor (5 m thick), an equivalent of c. 12 m can thus be expected in the Middle Vistula River Valley section. However, the record of *Bln. vistulensis* for the Raj N quarry suggests a thickness between 18 and 27 m for the *vistulensis* Zone in the Middle Vistula River Valley section, which is well above what could be expected on the basis of sedimentation rates. This implies that either *Bln. vistulensis* would appear earlier in the Middle Vistula River Valley than in the Kronsmoor section or that the sedimentation rate at Kronsmoor during the *vistulensis* Zone (*pseudobtusa* Zone of Schulz 1979) was considerably reduced relative to the Middle Vistula River Valley section.

THE POSITION OF THE TERCIS-DEFINED BASE OF THE MAASTRICHTIAN IN THE MIDDLE VISTULA RIVER VALLEY SECTION

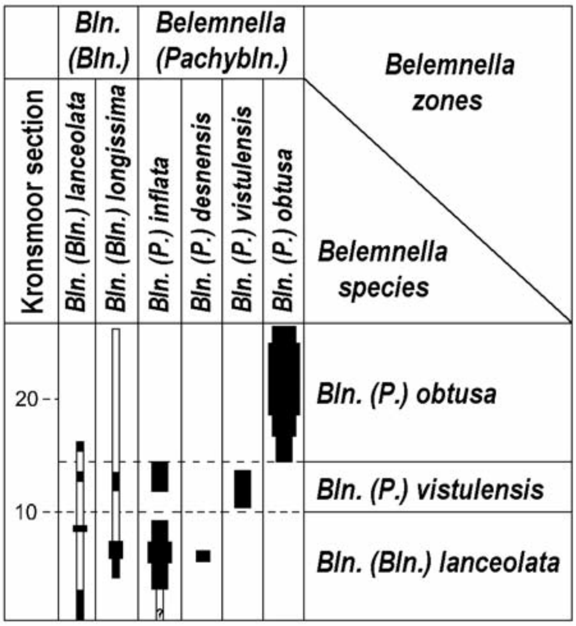
The Campanian–Maastrichtian boundary in the stratotype section at Tercis les Bains (southwest France) is defined as an arithmetic mean of 12 bioevents and corresponds to the 115.2 m level at that section (Odin and Lamaurelle 2001). A first attempt to identify the Tercis-defined Campanian–Maastrichtian boundary in the Middle Vistula River Valley section was performed by Walaszczyk (2004), on the basis of inoceramid bivalves. At Tercis, the boundary falls within the uppermost part of the "*Inoceramus*" *redbirdensis* Zone. According to Walaszczyk *et al*. (2002), the base of the overlying *Endocostea typica* Zone at level 117.1 m would be a good proxy for the stage boundary. In the Middle Vistula River Valley section, the base of the *E. typica* Zone is best exposed at Kłudzie S. According to Walaszczyk (2004, p. 108), the Tercis based Campanian–Maastrichtian boundary "…should be located in the interval between the LO of "*I.*" *redbirdensis* and the FO of *Endocostea typica*. The stratigraphically highest "*I.*" aff. *redbirdensis* was found 70 cm below, and the first *E. typica* about 8 m above the 'boundary marl'. Based on the prediction from the correlation between Tercis and the Middle Vistula River Valley section, the boundary would lie about 2 meters below the FO of *E. typica*, and about 6 metres above the 'boundary marl'."

The ammonite constraints on the Campanian-Maastrichtian boundary definition in the Middle Vistula River Valley section were recently published by Machalski (2012). This author noted that the FAD of *Pachydiscus neubergicus* (von Hauer, 1858) at Tercis coincides with the boundary level (uppermost "*I.*" *redbirdensis* Zone *sensu* Walaszczyk *et al*. 2002), while the FAD of *Diplomoceras cylindraceum* (Defrance, 1816) at Tercis is within the "*I.*" *redbirdensis* Zone. In the Middle Vistula River Valley section, the stratigraphically oldest *in situ*-collected specimen of *P. neubergicus* comes from the bottom of the Dziurków succession (*Endocostea typica* Zone of Walaszczyk 2004 and lower *Bln. obtusa* Zone, herein), but imprecisely located specimens from the sections of Kłudzie and Kamień North imply the presence of this species possibly in the upper part of the "*I.*" *redbirdensis* Zone of Walaszczyk (2004) (*Bln. vistulensis* Zone as interpreted here), thus well in agreement with Tercis. *D. cylindraceum* appears in the Middle Vistula River Valley section (Piotrawin) already within the "*Inoceramus*" *inkermanensis* Zone of Walaszczyk (2004), which is considerably below the FAD of this species at Tercis (Machalski 2012).

Recently, Niebuhr *et al*. (2011) attempted to identify the Lower Maastrichtian boundary position in the Kronsmoor section. Based on ammonite evidence, those authors proposed to place the base of the Maastrichtian Stage at Kronsmoor c. 11 m above flint layer F 600, between the FAD of *Diplomoceras cylindraceum* (Defrance, 1816) and that of *Pachydiscus neubergicus* (von Hauer, 1858). Confirmation for the correlation of the Campanian–Maastrichtian boundary as defined at Tercis with the level at +11 m above F 600 may be deduced from data presented by Thibault *et al*. (2012). Close to the Campanian–Maastrichtian boundary (CMB), those authors described a negative $\delta^{13}C$ excursion, in three distinct steps (CMB a, CMB b and CMB c), at Tercis les Bains, Stevns-1 and Rørdal. "A two-step 0.6‰ negative shift (CMB a and CMB c) is ... separated by a small rebound (CMB b).... The CMB as defined in Tercis falls almost exactly in the middle of CMB c" (Thibault *et al*. 2012, p. 81). At Kronsmoor, the decrease of $\delta^{13}C$ values (CMB a) starts at c. 6 m below the base of the *lanceolata* Zone (Niebuhr *et al*. 2011), while CMB c seems to correspond with a conspicuous negative shift of $\delta^{13}C$ values between 10–12 m, proposing the position of the Campanian–Maastrichtian boundary at Kronsmoor at the level of c. 11 m above flint layer F 600, as outlined by Niebuhr *et al*. (2011). This 11 m level corresponds to c. 1 m above the base of the *Bln. vistulensis* Zone (= *pseudobtusa* Zone *sensu* Schulz 1979) and the *Bln. obtusa* Superzone *sensu* Remin (*in* Niebuhr *et al*. 2011) at Kronsmoor. In the Vistula River Valley section, the base of the *Bln. obtusa* Superzone *sensu* Remin was documented at the top of the 'boundary marl' (Niebuhr *et al*. 2011; Remin 2012), which is generally well in line with the proposal made by Walaszczyk (2004).

While at Kronsmoor the base of the *Bln. vistulensis* Zone (= *pseudobtusa* Zone *sensu* Schulz 1979) and that of the *Bln. obtusa* Superzone *sensu* Remin are at the same level, the base of the former in the Middle Vistula River Valley section is distinctly lower (Solec Opoka; Raj N quarry). This quarry has also produced *Trochoceramus costaecus* (Khalafova, 1966) in the lower part of the section, in addition to representatives of "*Inoceramus*" *redbirdensis* Walaszczyk, Cobban and Harries, 2001. This implies that *Bln. vistulensis* first appears in the Middle Vistula River Valley section in the latest Campanian (definition of the Campanian-Maastrichtian boundary as based in Tercis) within the *T. costaecus* or "*I.*" *redbirdensis* zones *sensu* Walaszczyk (2004, p. 107). The correlation is confirmed independently by $\delta^{13}C$ studies in the Middle Vistula River Valley (Silke Voigt, personal communication 2012).

Accepting the level of c. 11 m above flint layer F 600 in the Kronsmoor section as the Campanian–Maastrichtian boundary, the belemnite species record of Schulz (1979) does not indicate a distinct change of species close to the boundary level, except of the FAD of *Bln. vistulensis* c. 1 m below the boundary (Text-fig. 3). However, in the Middle Vistula River Valley section *Bln. vistulensis* in line with the species concept of Schulz (1979) already appears in the latest Campanian as indicated by the presence of *T. costaecus* and "*I.*" *redbirdensis* at Raj N. As a consequence, the position of the Campanian–Maastrichtian boundary cannot be precisely localized using the species concept of Schulz.



Text-fig. 3. Belemnite record *sensu* Schulz (1979) of the topmost Campanian and lowermost Maastrichtian in the Kronsmoor section. Modified after Schulz (1979)

Based on the assumption of constant sedimentation rates in the Middle Vistula River Valley and Kronsmoor sections, the approximate position of the Campanian–Maastrichtian boundary may be estimated. In case 35 m in the Middle Vistula River Valley section correspond to 15 m in the Kronsmoor section, 4 m in Kronsmoor would equal c. 9–10 m in the Middle Vistula River Valley section. As a consequence, the Campanian–Maastrichtian boundary should be situated c. 9–10 m below the base of the section exposed at Dziurków, implying a position rather above than below the 'boundary marl' (compare Text-fig. 2). The result of this calculation is well in line with the proposal of Walaszczyk (2004), who placed the boundary c. 6 m above the 'boundary marl'.

TEMPERATURE-RELATED APPEARANCE AND DISAPPEARANCE OF BELEMNITE SPECIES IN THE CAMPANIAN–MAASTRICHTIAN BOUNDARY INTERVAL AT KRONSMOOR

Oxygen stable isotope data from bulk sediment or foraminiferal tests have frequently been interpreted with respect to changes of seawater temperature (Friedrich *et al*. 2009). On a larger scale, they may be indicative of global climate change in addition to palaeoceanographical reorganisations, the latter affecting not only regional water temperature but also ocean palaeocirculation (Vonhof *et al*. 2011). Niebuhr *et al*. (2011, table 1) published oxygen isotope data for the Kronsmoor section, from which palaeotemperature values were gauged by using the equation of Anderson and Arthur (1983). The palaeotemperature values have been recalculated here (Table 1) and related to the belemnite record at Kronsmoor. However, occurrences of isolated guards, here interpreted as stray specimens, were not considered in this analysis. Based on data supplied by Niebuhr *et al.* (2011) the preferred temperature range and a so-called "mean temperature" were derived for each species (Table 2).

The species characterised by the lowest mean temperature is *Bln. desnensis sensu* Schulz (1979) which is confined to a very narrow interval within the *lanceolata* Zone. The observed temperature range for this species equals that of *Bln. longissima*. However, the latter species has a longer range than *Bln. desnensis*, which is reflected by the slightly higher mean temperature of 17.6 versus 17.5 °C. The commonest belemnite in the *lanceolata* Zone of Kronsmoor is *Bln. inflata*. Its temperature range is slightly wider than that of *Bln. longissima* and the calculated mean temperature of 17.8 °C for this species may indicate a slightly higher optimum temperature. *Belemnella lanceolata* has not been recorded from levels with a temperature below 17.0 °C, differing in this respect from species of *Belemnella* mentioned above. Its mean temperature of 18.0 °C is the highest of all species recorded from the *lanceolata* Zone. A very similar mean temperature preference is shown by *Bln.* cf. *praearkhangelskii* Naidin, 1964. Of note is that the temperature range tolerated by this species is the greatest of all, with the exception of *Bln. sumensis* Jeletzky, 1949. *Belemnella vistulensis* is not recorded from levels with a mean temperature below 17.3 °C. The mean temperature of this belemnite species, which predomi-

Relative depth of sample [m +/- 0.1 m]	Calculated temperature [°C]	Moving average [°C]	Temperture change [°C]	Belemnite record
47	18.9	19.2	-0.5	
46	19.4	19.0	0.8	
45	18.6	19.0	-0.5	
44	19.0	19.2	-1.0	
43	20.0	19.4	0.8	
42	19.2	19.6	-0.6	
41	19.7	19.3	0.8	
40	18.9	19.7	-1.7	
39	20.6	19.6	1.4	
38	19.2	19.8	-0.3	last *Bln.* cf. *praearkhangelskii*
37	19.5	18.8	1.9	
36	17.6	***17.5***	2.3	
35	***15.4***	***17.0***	***-2.7***	first *Bln.* cf. *praearkhangelskii*
34	18.1	***17.2***	0.1	
33	18.0	18.2	-0.5	
32	18.5	18.7	-1.1	
31	19.6	19.4	-0.4	
30	20.0	19.7	0.7	
29	19.4	19.4	0.6	
28	18.7	18.8	0.5	
27	18.2	18.7	-0.9	
26	19.1	18.7	0.5	
25	18.7	19.1	-0.8	
24	19.4	19.0	0.4	
23	19.0	18.8	1.1	
22	18.0	18.6	-0.8	
21	18.7	18.5	0.0	
20	18.7	18.8	-0.3	
19	19.0	18.9	-0.1	
18	19.1	18.8	0.8	
17	18.3	18.5	0.0	
16	18.3	18.4	-0.3	
15	18.6	18.8	-1.1	first *Bln. obtusa*
14	***19.7***	18.5	***2.4***	last *Bln. vistulensis* and *Bln. inflata*
13	17.3	18.5	-1.4	
12	18.7	18.4	-0.6	re-appearance of *Bln. inflata*
11	19.3	19.0	0.4	first *Bln. vistulensis*
10.5	18.9	18.9	0.4	
10	***18.5***	18.0	***2.0***	
9.5	***16.5***	***17.5***	-1.1	
9	17.5	***17.1***	0.2	last representatives of *Bln.*
8.5	17.3	***17.3***	0.3	
8	17.0	***17.4***	-0.8	
7.5	17.8	***17.3***	0.9	
7	***16.9***	***17.1***	0.3	interval with
6.5	***16.7***	***17.5***	***-2.1***	*Bln. desnensis*
6	18.8	17.9	0.6	*sensu* Schulz

Table 1a. Calculated palaeotemperatures (after Niebuhr *et al.* 2011) and temperature change in the Kronsmoor section compared with the belemnite record

nates in the *vistulensis* Zone at Kronsmoor, is as much as 0.6 °C higher than that of *Bln. inflata*. The recorded temperature range for *Bln. obtusa* is narrower than that of *Bln. vistulensis*, but the maximum temperatures of both species are similar. The difference is reflected by the mean temperature of *Bln. obtusa*, which is as much as 0.9 °C higher than that of *Bln. inflata*. *Belemnella sumensis* seems to have adapted to even higher temperatures than *Bln. obtusa*. The temperature values of *Bln. gracilis* resemble those of *Bln. sumensis*. Nevertheless, it may be assumed that *Bln. gracilis* preferred even higher temperatures than *Bln. sumensis*, because

Relative depth of sample [m +/- 0.1 m]	Calculated temperature [°C]	Moving average [°C]	Temperture change [°C]	Belemnite record
5.5	18.2	18.1	0.9	
5	17.4	***17.6***	0.2	last single representatives of typical Campanian species of *Belemnitella*
4.5	17.2	***17.3***	0.0	
4	17.3	***17.1***	0.3	regular occurrence of *Bln.*; first *Bln. longissima*
3.5	***17.0***	***17.6***	-1.7	
3	18.7	18.1	0.0	
2.5	18.7	18.3	1.3	
2	17.4	18.3	-1.2	
1.5	18.6	18.2	0.0	
1	18.6	18.3	0.8	
0.5	17.8	18.4	-1.1	
0	18.9	18.4	0.4	first *Bln. lanceolata*
-0.5	18.5	18.4	0.9	
-1	***17.6***	***17.6***	0.9	
-1.5	***16.7***	***17.8***	***-2.3***	
-2	19.0	18.3	-0.1	
-2.5	19.1	18.9	0.5	
-3	18.6	18.7	0.2	
-3.5	18.4	18.7	-0.6	
-4	19.0	18.6	0.6	
-4.5	18.4	18.6	0.0	
-5	18.5	18.4	0.2	disappearance of regular *Blt. schulzi*
-5.5	***18.3***	19.2	***-2.7***	
-6.5	21.0	19.7	1.1	
-7.5	19.8	20.7	-1.5	
-8.5	21.4	20.7	0.4	
-9.5	21.0	20.8	0.9	
-10.5	20.1	20.1	0.8	
-11.5	19.2	19.3	0.5	
-12.5	18.7	19.3	-1.3	
-13.5	20.0	20.0	-1.2	
-14.5	21.2	20.7	0.2	
-15.5	21.0	20.9	0.4	
-16.5	20.6	20.2	1.5	
-17.5	19.1	20.2	-1.7	
-18.5	20.8	19.8	1.1	
-19.5	19.7	19.4	1.9	basis of *grimmensis*/*granulosus* Zone
-20.5	***17.7***	19.4	***-3.1***	
-21.5	20.8	19.4	1.0	
-22.5	19.8	20.0	0.3	
-23.5	19.5	19.8	-0.5	
-24.5	20.1	19.7	0.7	

Table 1b. Calculated palaeotemperatures (after Niebuhr *et al.* 2011) and temperature change in the Kronsmoor section compared with the belemnite record

this species is predominant in more southerly sections of the Ultrahelveticum near Siegsdorf, Bavaria (Schulz and Schmid 1983). For comparison, the temperature range and mean temperature of *Belemnitella schulzi* Christensen, 2000 from the *grimmensis*/*granulosus* Zone of Kronsmoor are shown (Table 2). The latter (20.0 °C) represents the highest value for all belemnite species listed in the table.

The appearance and disappearance of belemnite species in the Kronsmoor section is closely linked to the course of the temperature recorded by Niebuhr *et al*. (2011). *Belemnitella schulzi* disappeared about 5 m below the top of the *grimmensis*/*granulosus* Zone *sensu germanico* (Christensen 2000). This LAD (last appearance datum) coincides with a distinct and lasting temperature drop (event 1 in Text-fig. 4; corresponding approximately to the base of CAB a of Thibault *et al*. 2012). However, *Blt. schulzi* seemingly adapted to the lower temperatures, as indicated by the presence of this species in the *jasmundi-acutirostris* brachiopod Zone, equivalent to the lower *lanceolata* Zone, in Denmark (Hvide Klint, Møn), where it is the sole belemnite species present (Christensen 1996, 2000). It may be concluded that further environmental factors contributed to the absence of *Blt. schulzi* and of other belemnite species in the upper 5 m of the *grimmensis*/*granulosus* Zone at Kronsmoor. As a matter of fact, rare representatives of the genus *Belemnitella* are known from the interval from 0 to +5 m (lower *lanceolata* Zone) at Kronsmoor, co-occurring with the first representatives of the genus *Belemnella* (Schulz 1982), indicating an improvement in conditions for the genus *Belemnitella*.

The FADs of *Bln. lanceolata* and possibly also of *Bln. inflata* at the 0 m level in the Kronsmoor section mark the second event (event 2 in Text-fig. 4). Because early representatives of the genus *Belemnella* were seemingly better adapted to lower temperatures than local members of *Belemnitella* (Table 2), the hypothesis may be put forward that the distinct temperature decrease detected at –1.5 m below level F600, may have triggered the range extension of the genus *Belemnella* preferably from the north (and/or east) to the south (and/or west). Nevertheless, the appearance of *Belemnella* does not necessarily represent an immediate effect of the drop in temperature. The effect could also be indirectly associated with changes of ocean palaeocirculation or a combination of both.

Representatives of the genus *Belemnella* are comparatively rare in the lower 4 metres of the *lanceolata* Zone. They become more common immediately after a distinct temperature drop detected at the +3.5 m level. This decrease is also related to the FAD of *Bln. longissima* at the +4 m level (event 3 in Text-fig. 4).

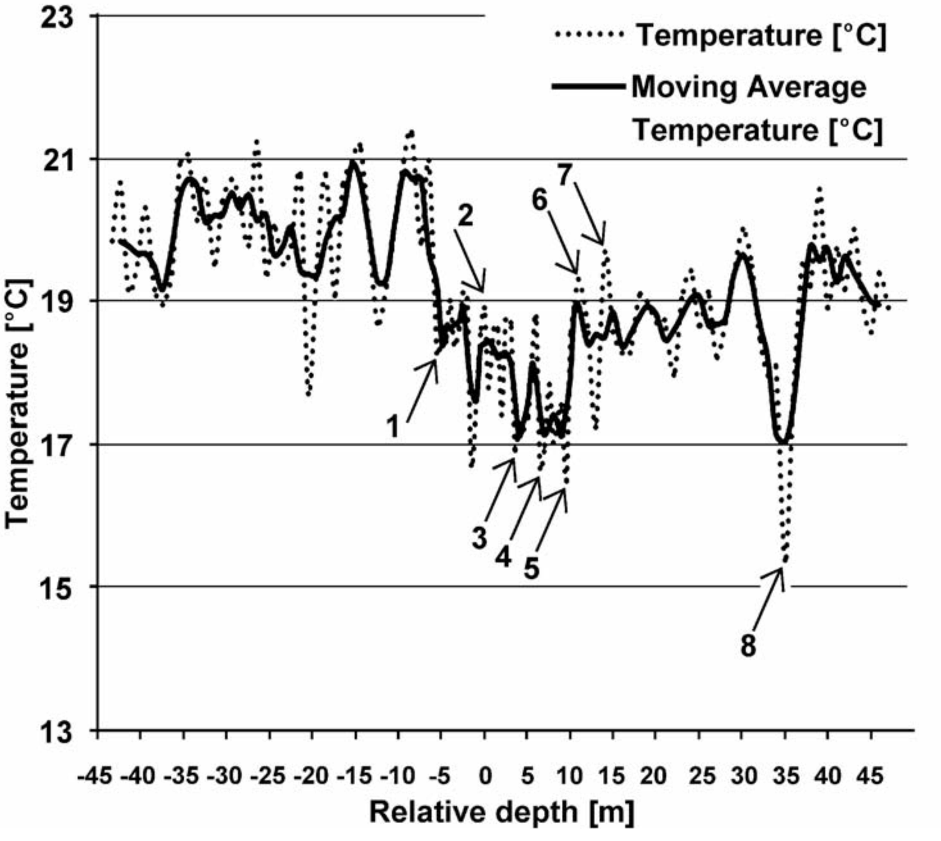
Belemnite species	Mean temperature of the documented levels, where the species is recorded from [°C]	Maximum value of temperature [°C]	Minimum value of temperature [°C]
Bln. desnensis	17.5	18.8	16.7
Bln. longissima	17.6	18.8	16.7
Bln. inflata	17.8	18.9	16.7
Bln. inflata (0-6.0, 12-14 m)	18.0	18.9	17.0
Bln. inflata (6.5-9 m)	17.2	17.8	16.7
Bln. cf. *praearkhangelskii*	17.9	19.5	15.4
Bln. lanceolata	18.0	18.9	17.0
Bln. vistulensis	18.4	19.3	17.3
Bln. obtusa	18.7	19.4	18.0
Bln. sumensis	18.9	20.6	15.4
Bln. gracilis	18.9	20.0	18.0
Blt. schulzi	20.0	21.4	18.3

Table 2: Calculated mean palaeotemperatures, plus maximum and minimum palaeotemperatures for the environment of the species of *Belemnella* and *Belemnitella* in the Kronsmoor section deduced from the data shown in Table 1

When the genus *Belemnella* became common in the Kronsmoor section, the genus *Belemnitella* was ousted, with the exception of *Blt. pulchra* Schulz, 1982. Hence, replacement of *Belemnitella* by *Belemnella* during the latest Campanian (definition of the Campanian-Maastrichtian boundary as based in Tercis) may be considered to have been a process of long duration, which could be associated with a sustainable temperature decrease of about 2 °C.

The last two-thirds of the *lanceolata* Zone were characterised by the lowest temperatures during the latest Campanian, with two minima of 16.7 °C and 16.5 °C at the +6.5 and +9.5 m levels. The first minimum coincided with the presence of *Bln. desnensis* (Jeletzky, 1941), which was considered to be synonymous with *Bln. licharewi* (Jeletzky, 1941) by Schulz (1979). *Belemnella licharewi* is known mainly from the Central Russian Subprovince of the North European palaeobiogeographical province, where it is the index species of the oldest *Belemnella* zone. The short-term appearance of *Bln. desnensis sensu* Schulz was probably triggered by a temperature decrease (event 4 in Text-fig. 4), but this species could not assert itself in the medium term against *Bln. inflata.*

Significant temperature changes were observed between the levels +9.5 and +11 m (events 5 and 6 in Text-fig. 4). At +9.5 m, the temperature fell by 1.1 °C to 16.5 °C, then increased by 2.0 °C to 18.5 °C and subsequently to a maximum of 19.3 °C at the +11 m level (Table 1). Of note, according to Remin (*in* Niebuhr *et al*. 2011), it is the interval between +9 m and +11 m at Kronsmoor, which did not produce any belemnites, indicating that belemnite species in the Kronsmoor area were significantly impacted by this environmental change. At the same level between +9.5 and +11.0 m, a distinct negative shift in $\delta^{13}C$ occurs (Voigt *et al.* 2010; Niebuhr *et al.* 2011). The most straightforward interpretation would be to link the shift with a sea level fall. Alternatively, the generation of a negative carbon isotope excursion could



Text-fig. 4. Estimates of palaeotemperature for the Kronsmoor section based on data published by Niebuhr *et al*. (2011). The X-axis indicates sample provenance (–45 to –20 m: *langei* Zone; –20 to 0 m: *grimmensis*/*granulosus* Zone; 0 to +10 m: *lanceolata* Zone; +10 to +15 m: *vistulensis (=pseudobtusa)* Zone; +15 to +28 m: *obtusa* Zone; +28 to +50 m: *sumensis* Zone (Schulz 1979). The arrows numbered 1 to 8 indicate the following distinct palaeoevents: Event 1: Disappearance of *Blt. schulzi* and distinct drop in palaeotemperature; Event 2: The FAD of *Bln. lanceolata* and possibly also of *Bln. inflata;*Event 3: *Belemnella* comparatively common following a distinct temperature drop. FAD of *Bln. longissima*; Event 4: Short-term appearance of *Bln. desnensis*; Events 5 and 6: Distinct temperature fluctuations (first a decrease followed by a distinct increase), associated with a turnover in belemnite populations; Event 7: LAD of *Bln. vistulensis* and *Bln. inflata*; FAD of *Bln. obtusa*; Event 8: Distinct temperature decrease; FAD of *Bln.* cf. *praearkhangelskii* be related to the rapid dissociation of gas hydrates in continental margin sediments. The reasons and consequences of such releases are not yet fully understood, but may include carbonate dissolution as well as increased atmospheric CO_2 concentrations leading to climatic warming (Jarvis 2002). Such kind of a methane-driven reduction of $\delta^{13}C$ values represents usually a short-term episode in the order of 100 kyr. In addition, a pulse of volcanically derived CO_2 is also a potential explanation for the negative shift in $\delta^{13}C$ and the subsequent temperature increase, but this would require a major volcanic episode (Jarvis 2002), for which there is no evidence. In summary, the relationship between the $\delta^{13}C$ shift and the cooling period documented between the –6.5 m and +9.5 m levels and the rapid warming at the Campanian–Maastrichtian boundary [Tercis definition] is not fully understood to date. Apparently, the temperature drop documented at +9.5 m significantly reduced belemnite populations in the Kronsmoor area, while the subsequent rapid temperature increase up to 19.3 °C at +11 m resulted in almost total extirpation of species in that region. The first species observed after this event in the Kronsmoor section is *Bln. vistulensis*.

Belemnella inflata repopulated the Kronsmoor area slightly later than *Bln. vistulensis*. Of note is the fact that in this area different stratigraphic forms of *Bln. inflata* may be distinguished (Schulz 1979, table 3), which are also characterised by different temperature preferences. Those from the *lanceolata* Zone *sensu germanico* were referred to forma anterior (f.a.) 1 and 2, those from the *vistulensis* Zone (*pseudobtusa* Zone *sensu germanico*) to forma posterior (f.p.) 1 and 2. The differences between f.a. and f.p. are slight (i.e., cross-sectional shape of guards at the protoconch). More significantly, both forms f.a. and f.p. represent independent evolutionary lineages of *Bln. inflata*, because in both lineages an evolution towards less lanceolate and slightly shorter forms is documented, allowing the separation at Kronsmoor of f.a.1 and f.a.2 on the one hand and of f.p.1 and f.p.2 on the other. Worth mentioning is also that *Bln. inflata* f.p.1 resembles *Bln. inflata* f.a.1, rather than *Bln. inflata* f.a.2, which led Schulz (1979, p. 51) to the conclusion that *Bln. inflata* invaded the Kronsmoor area during *vistulensis* Zone time (i.e., *pseudobtusa* Zone *sensu germanico*) entering from a region where the evolution from *Bln. inflata* f.a.1 to *Bln. inflata* f.a.2 did not occur. To this interpretation we can add further pieces of evidence: when *Bln. inflata* f.a.1 first appeared in the Kronsmoor area, the temperature was comparatively high. During the lower 6 m of the *lanceolata* Zone the mean temperature value accounted for c. 18.1 °C. However, from +6.0 to +9.5 m above level F600, temperature dropped (mean value c. 17.1 °C). At the beginning of this cooling period, *Bln. desnensis sensu* Schulz appeared, a species presumably better adapted to lower temperatures than *Bln. inflata* f.a.1. Nevertheless, *Bln. inflata* f.a.1 was able to adapt to the environmental change and, hence, was not ousted by *Bln. desnensis*, while the latter species became extinct in the Kronsmoor area at +7 m. *Belemnella inflata* f.a.2, however, died out during the temperature fluctuations close to the Campanian–Maastrichtian boundary. The forms of *Bln. inflata* f.p., reinvading the Kronsmoor region during the *vistulensis* Zone (+12 to +15 m), were again adapted to higher temperatures (mean value c. 18.5 °C). This temperature preference is well in line with that of *Bln. inflata* f.a.1. Similarly, the morphological features of *Bln. inflata* f.p.1 from the *vistulensis* Zone (*pseudobtusa* Zone *sensu germanico*) resembled those of *Bln. inflata* f.a.1, but not those of *Bln. inflata* f.a.2 of the *lanceolata* Zone (compare Schulz 1979, figs 41–47), indicating that *Bln. inflata* f.p.1 must be closely related to *Bln. inflata* f.a.1. As a consequence, *Bln. inflata* f.a.2 may be interpreted as a short-lived offshoot of the original *Bln. inflata* that was adapted to cooler temperatures.

The next distinct temperature fluctuation in the Kronsmoor succession is noted between +14 and +15 m, when *Bln. vistulensis* and *Bln. inflata* died out and *Bln. obtusa* first appeared (event 7 in Text-fig. 4). Most significant is the temperature maximum of 19.7 °C that almost coincided with the disappearance of *Bln. vistulensis*. Schulz (1979) proposed the following scenario: *Bln. vistulensis* became extinct at the +14.5 m level, while *Bln. inflata* developed quickly towards *Bln. obtusa*. It can be concluded that temperature fluctuations, and the temperature maximum in particular, interfered with the occurrence of species of the genus *Belemnella*, thus exerting a distinct selective pressure on belemnite populations.

The last distinct temperature decrease, documented in the Kronsmoor section, occurred within the *sumensis* Zone, when temperatures suddenly dropped by as much as 2.7 °C, from 18.1 to 15.4 °C (event 8 in Text-fig. 4). The temperature minimum coincided with the FAD of *Bln*. cf. *praearkhangelskii*. This species was originally described from the Ukraine, the Saratov area in Russia (Naidin 1975), western Kazakhstan and Azerbaijan in the Central Russian Subprovince (Schulz 1979). The temperature preferences of this species are difficult to interpret on the basis of data available from Kronsmoor, because it was obviously able to survive a rapid temperature increase of as much as 4.2 °C (Table 1). Two scenarios are thus possible: either the ‘original’ *Bln*. cf.

praearkhangelskii preferred a cooler climate, but adapted rapidly to the warmer conditions in the Kronsmoor region, or this species was already able to tolerate a comparatively wide temperature range, such as e.g. *Bln. sumensis* Jeletzky, 1949 (compare Table 2). In the latter case, the appearance of *Bln*. cf. *praearkhangelskii* in the Central European Subprovince cannot be seen as an immediate effect of the temperature decrease, but can be understood as an indirect consequence, for instance, of changes of ocean palaeocirculation, supporting migration from the Central Russian to the Central European Subprovince. In this context, two migration pathways must be considered: the first, more probable, from the east, via Poland, and the second, from the north via Sweden and possibly England (Keutgen 2011). Although *Bln*. cf. *praearkhangelskii* is known from as far west as northeast Belgium, it is recorded only from a limited time interval, from the middle *sumensis* Zone, in the Central European subprovince. The reason for this limited appearance is not yet clear.

CORRELATION OF THE KRONSMOOR AND MIDDLE VISTULA RIVER VALLEY SECTIONS

The first event that can be identified in the Middle Vistula River Valley section within limits of stratigraphic resolution is the appearance of *Belemnella* sp. in the Raj section; this is correlated with event 2 in the Kronsmoor section, which is the FAD of *Bln. lanceolata*.

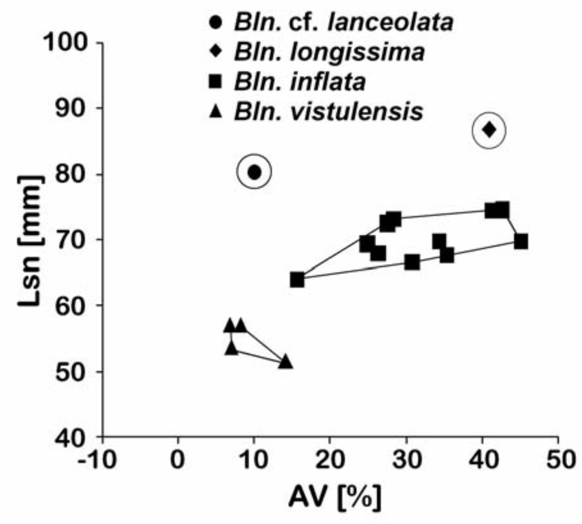
The appearance of *Bln. longissima* in the Raj N section marks event 3 of the Kronsmoor section. In addition, the mean values of the population of *Bln. inflata* from Raj N resemble those of *Bln. inflata* f.a.1 at Kronsmoor from the interval 0 to +7 m. Hence, it may be concluded that equivalents of the interval +4 to +7 m in Kronsmoor are exposed in the Raj N section.

The events 5 and 6 of Kronsmoor are difficult to identify unequivocally in the Middle Vistula River Valley section. Event 5 corresponds with the temporary absence of *Bln. inflata* in the Kronsmoor section, while event 6 coincides with the appearance of *Bln. vistulensis*. In the Middle Vistula River Valley section the first representatives of *Bln. vistulensis sensu* Schulz (1979) appear in the Raj N section, where they represent a small but distinct group (Text-fig. 5), differing from the dominating *Bln. inflata* in their less lanceolate shape, shorter standardized length, larger alveolar angle and larger Schatzky distance. Neither is information available, from which level(s) the specimens of *Bln. vistulensis* derived, nor whether or not they co-occur with *Bln. inflata*. With respect to *Bln. inflata*, the available, though limited, records of that species from deposits younger than those exposed in the Raj N section point to its disappearance at the level around the 'boundary marl'. However, at the localities Podole, Kłudzie S, and Kłudzie N, where the 'boundary marl' is exposed, *Bln. inflata* is already rare (Text-fig. 6). With respect to the events 5 and 6 the available preliminary data allow to folmulate two alternative hypotheses:

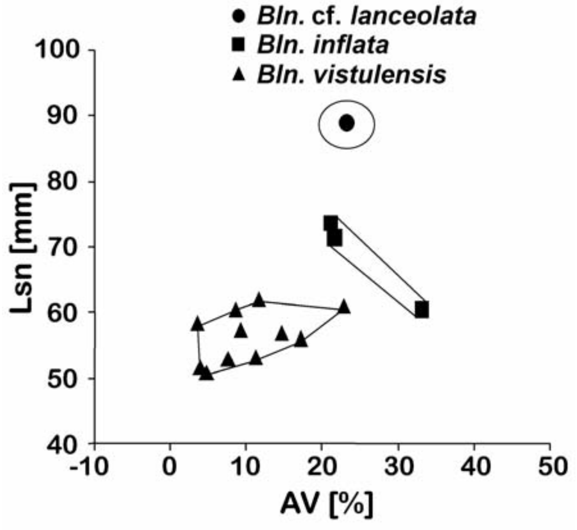
– Event 5/6 of Kronsmoor is marked by the FAD of *Bln. vistulensis* in the Raj N section. *Bln. inflata* occurs sporadically in the *vistulensis* Zone of the Middle Vistula River Valley section.

– Event 5/6 of Kronsmoor is marked by the disappearance of *Bln. inflata* close to the 'boundary marl' in the Middle Vistula River Valley. This interpretation would, however, imply that *Bln. vistulensis sensu* Schulz (1979) appears already within equivalents of the *lanceolata* Zone of Kronsmoor in the Middle Vistula River Valley section.

Additional, well horizonted collected belemnite material from the Middle Vistula River Valley is necessary to decide in favour of one of both hypotheses. Worth of note, the results of Remin (2012, this issue) and the preliminary ones of Silke Voigt would argue for the second interpretation. Considering stable sedimentation rates in the Kronsmoor and the Middle Vistula River Valley sections, the position of event 5 at +9 m and of event 6 at +11 m in Kronsmoor should be expected at c. 14 m (event 5) and c. 9 m (event 6) below the base of the Dziurków section, respectively. This calculation also favours the second interpretation, because the latest records of *Bln. inflata* (event 5) have been collected close to the 'boundary marl', which is situated approximately 15 m below the base of the Dziurków section (Text-fig. 2). The rather limited material of *Bln. inflata* available from below the 'boundary marl' at Kłudzie N does not allow drawing a final conclusion, but the slightly advanced shape of these specimens corresponds well with *Bln. inflata* f.a.2 from the interval +7 to +9 m at Kronsmoor. In addition, *Bln*. cf. *lanceolata* has been identified from Kłudzie N below the 'boundary marl', which recalls the presence of *Bln. lanceolata* in the interval +8 to +9 m in Kronsmoor. Although it cannot be ruled out completely that sedimentation rates in the Middle Vistula River Valley section changed relative to the Kronsmoor section during the latest Campanian and earliest Maastrichtian – which is why this calculation must be considered with reservation – the available information favours the conclusion that the FAD of *Bln. vistulensis* in the Middle Vistula River Valley section most probably predates the FAD of this species in the Kronsmoor section.



Text-fig. 5. Relationship AV *vs* Lsn in *Bln.* cf. *lanceolata*, *Bln. longissima*, *Bln. inflata* and *Bln*. *vistulensis* from the Solec Opoka of the Raj N quarry



Text-fig. 6. Relationship AV *vs* Lsn in *Bln.* cf. *lanceolata*, *Bln. inflata* and *Bln*. *vistulensis* from the *vistulensis* Zone of the Solec and Dziurków opokas of the sections Podole, Kłudzie S, and Kłudzie N

The last event that can be identified in the Kronsmoor and in the Middle Vistula River Valley sections, is the FAD of *Bln. obtusa*. However, the precise level of this event (event 7) has not been defined in the Middle Vistula River Valley section. Nevertheless, representatives of *Bln. obtusa* from Dziurków are early forms of this species as understood by Schulz and are best compared with those occurring between +15 and +17 m in the Kronsmoor section. This implies that the base of the *obtusa* Zone should be exposed close to the quarry floor at Dziurków.

CONCLUSION

In the Campanian–Maastrichtian boundary interval of the Middle Vistula River Valley section three zones of *Belemnella* can be distinguished using the species concept of Schulz (1979). These are, in ascending order, the *lanceolata*, *vistulensis* and *obtusa* zones. While the bases of the *lanceolata* and *obtusa* zones in the Kronsmoor and Middle Vistula River Valley sections can be easily correlated, the base of the *vistulensis* zones (*Bln. vistulensis* according to the concept of Schulz, 1979) in both sections is probably diachronous.

The appearance and disappearance of species of the genus *Belemnella* in the Kronsmoor section are closely related and indicative of palaeotemperature and/or oceanic circulation changes. Eight events are distinguished in the Kronsmoor section; three of these could be traced in the Middle Vistula River Valley section as well. These allow a relatively detailed correlation of the Kronsmoor and Middle Vistula River Valley section using Schulz's species concept of *Belemnella*.

The concept for species identification of the genus *Belemnella* proposed by Remin (2007, 2008 and 2012) has resulted in a similar correlation of the Kronsmoor and Middle Vistula River Valley sections. The most striking difference represents the fact that the species concept of Schulz (1979) hinted at an earlier appearance of *Bln. vistulensis* than it is revealed using the concept of Remin (2012).

SYSTEMATIC PALAEONTOLOGY
(by N. Keutgen)

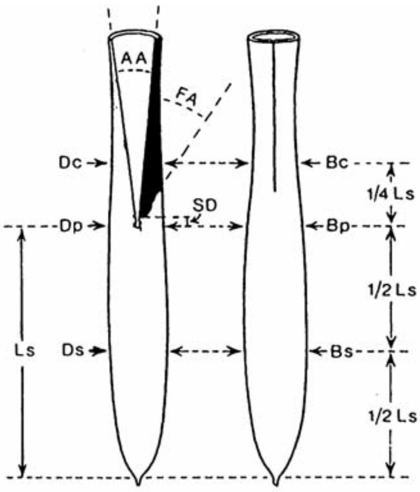
Terminology of the guard, measured characters and abbreviations

Systematics, terminology and methods to describe guards of the genus *Belemnella* follow Schulz (1979) with respect to the shape and standardised length of the guard and Christensen (1995; 1999, figs 9, 14) for the internal characters but with the exception of SD (Text-fig. 7):

Bs – lateral diameter halfway between apex and protoconch (in mm)
Bp – lateral diameter at protoconch (in mm)
Bc – lateral diameter at rostrum cavum, ¼ Ls from protoconch (in mm)
Ds – dorsoventral diameter halfway between apex and protoconch (in mm)
Dp – dorsoventral diameter at protoconch (in mm)
Dc – dorsoventral diameter at rostrum cavum, ¼ Ls from protoconch (in mm)
Qp – Bp/Dp

WQs – ontogenetic growth quotient of individual guards, $WQs = (Ls2 - Ls1)/(Dp2 - Dp1)$ with $Dp2 > Dp1 > 6$ mm
Ls – length from apex to protoconch (in mm)
Lsn – standardised length form apex to the protoconch, $Lsn = Ls + WQs \times (13.5 - Dp)$ (in mm). In case WQs could not be determined, a value of WQs = 1.8 was used as recommended by Schulz (1979) for specimens from the lower Lower Maastrichtian
AV – ventral aspect ($AV = (Bs - Bc) \times 100/Bp$ in %)
AL – lateral aspect ($AL = (Ds - Dc) \times 100/Dp$ in %)
AVs – ventral aspect of rostrum solidum ($AVs = (Bs - Bp) \times 100/Bp$ in %)
ALs – lateral aspect of rostrum solidum ($ALs = (Ds - Dp) \times 100/Dp$ in %)
SD – Schatzky Distance, the distance (in mm) between the midpoint of the protoconch and the posterior end of the ventral fissure measured along the axis of the guard
AA – alveolar angle, which is the dorsoventral angle (in °) between the walls of the alveolus measured in the medium plane about 10–15 mm from the protoconch
FA – fissure angle, which is the angle (in °) between the wall of the alveolus and the straight line connecting the intersection points of the bottom of the ventral fissure on the wall of the alveolus and the outer margin of the guard

All measurements of rostra were taken by Remin; for the exact procedure, the reader is referred to Remin (2012).



Text-fig. 7. Diagram illustrating morphological elements of the belemnite guard (ventral view at right, lateral view of a split guard at left). AA = Alveolar angle; FA = Fissure angle; SD = Schatzky Distance. Ls = Length from apex to protoconch. D = Dorso-ventral diameter. B = Lateral diameter. After Christensen (1988) and Keutgen (1997)

The following categories for size and shape of guards of the genus *Belemnella* are distinguished, following the definitions of Christensen (1995) and Christensen *et al.* (2004) for the genus *Belemnitella*:

Size – length from apex to protoconch <55 mm: small guard
– length between 55 and 65 mm: large guard
– length between 65 and 75 mm: very large guard
– length > 75 mm: extraordinary large guard
Shape – AV and AL larger than 30%: distinctly lanceolate guard
– AV and AL between 10 and 30%: slightly lanceolate guard
– AV and AL between –10 and 10%: subcylindrical guard
– AV and AL between –30 and –10%: subconical guard
– AV and AL smaller than –30%: conical guard

Because species identification within the genus *Belemnella* using the concept of Schulz (1979) can only be performed on (near-) complete guards, only these specimens have been used, with the exception of the oldest two representatives of *Belemnella*.

Repositories

Museum of the Faculty of Geology; specimens prefixed by ZI/65/abbreviations of the outcrop, e.g. ZI/65/Raj/001. The abbreviation for individual outcrops are as follows: Raj – Raj; Raj N – Raj N; Podole – Podole; Kłudzie S – KłudzS; Kłudzie N – KłudzN; Dziurków – Dziu.

Museum of the Geological and Paleontological Institute of the Universtity of Hamburg [Geologisch-Paläontologisches Institut Hamburg]; specimens prefixed by Kx/xxx and S/xxx; e.g. KK408.

Order Belemnitida von Zittel, 1895
Suborder Belemnopseina Jeletzky, 1965
Family Belemnitellidae Pavlow, 1914
Genus *Belemnella* Nowak, 1913
Subgenus *Belemnella* Nowak, 1913

Belemnella (*Belemnella*) cf. *lanceolata*
(von Schlotheim, 1813)

1813. *Belemnites lanceolatus* Schlotheim, p. 111.
1979. *Belemnella* (*Bln.*) *lanceolata* (Schlotheim, 1813); Schulz, p. 95, pl. 1, figs 1–9, text-fig. 54 (with additional synonymy).

1991. *Belemnella* (*Belemnella*) *lanceolata* (Schlotheim, 1813); Keutgen and van der Tuuk, p. 18, pl. 3, figs 1–2.
2007. *Belemnella longissima* Schulz, 1979; Remin, p. 108 (*pars*), pl. 1, figs 4–5, 7, 9–10, *non* pl. 1, figs 1–3, 6, 8.
2012. *Belemnella longissima* Schulz, 1979; Remin, p. 517 (*pars*), pl. 1, figs 9–10, *non* pl. 1, figs 1–8.

HOLOTYPE: Breynius 1732, tabula belemnitarum, figs. 7-9, as emphasized by Birkelund (1957, p. 37), Christensen (1975, p. 59), Schulz (1979, p. 96), and Riegraf (2000, p. 297). The *Locus typicus* is given as "Prussia", only.

MATERIAL: One specimen (ZI/65/Raj N/016) from Raj N; one specimen (ZI/65/Kłudz N/005) from Kłudzie N, Solec Opoka.

DESCRIPTION: The two guards of *Bln*. cf. *lanceolata* are very and extraordinary large, slightly lanceolate in ventral and subcylindrical and slightly lanceolate, respectively, in lateral view. SD, AA and FA are small (Table 3). Vascular markings are weakly developed or missing. The range of variation of Lsn versus AV is shown in Text-figs 5-6.

	ZI/65/Raj N/016	ZI/65/Kłudz N/005
Ls [mm]	73.0	86.0
Dp [mm]	9.4	11.9
Lsn [mm]	80.3	88.9
AV [%]	10.0	23.3
AL [%]	-0.3	13.9
SD [mm]	0.5	1.0
AA [°]	13	15
FA [°]	14	27

Table 3. Measurements of critical characters of *Belemnella* cf. *lanceolata* from the Solec Opoka

DISCUSSION: The range of variation of *Bln. lanceolata* from Balsvik (southern Sweden) is considered representative of this species (Schulz 1979). It is quite large and covers, otherwise, typical forms of *Bln. longissima* and *Bln. inflata.* The usual Lsn values for typical *Bln. lanceolata* vary between 72 and 82 mm, and AV values between 15 and 30%. In this respect, neither of the specimens recorded here represents typical *Bln. lanceolata*.

Specimen ZI/65/Kłudz N/005 is characterised by a very large Lsn value, which is otherwise typical of *Bln. longissima* Schulz, 1979. However, it differs from the latter in its less clavate shape in ventral view. This specimen does not plot within the range of *Bln. longissima* from Kronsmoor, but it is well within that of *Bln. lanceolata* from Balsvik, where such slender forms rarely occur. Consequently, ZI/65/Kłudz N/005 is referred to as *Bln.* cf. *lanceolata*.

Although the range of variation for AV and Lsn of *Bln. lanceolata* from Balsvik is comparatively large, specimen ZI/65/Raj N/016 does not plot within the range of AV documented for this species. Its AV is distinctly smaller than 15%. The combination of AV and Lsn would favour assignment to *Belemnella gracilis* (Arkhangelsky, 1912). Because *Bln. gracilis* is considered a stratigraphically younger form, which developed from *Bln. lanceolata* during the early Early Maastrichtian (Schulz 1979), this specimen is tentatively considered an extreme variant of *Bln. lanceolata*. Although Schulz (1979) and Schulz and Schmid (1983) included a single specimen from Podole, illustrated by Kongiel (1962, pl. 9, figs 7–9), in the synonymy of *Bln. gracilis*, most of Kongiel's specimens of *Bln. gracilis gracilis* are considered conspecific with *Bln. lanceolata*. However, this does indicate that *gracilis*-like forms of *Belemnella* (*sensu* Schulz and Schmid 1983) may be present around the Campanian–Maastrichtian boundary in the Middle Vistula River Valley section, but more material is needed to determine whether they represent a distinct species or should be regarded as extreme variants of *Bln. lanceolata*, as tentatively proposed herein.

DISTRIBUTION: *Belemnella lanceolata* is known from the uppermost Campanian *lanceolata* Zone to the lower Lower Maastrichtian *obtusa* Zone of the Central European and Central Russian Subprovinces. At Kronsmoor it occurs sporadically, but seems to be slightly commoner in the basal 3 metres of the *lanceolata* Zone and immediately below the top of this zone.

Belemnella (*Belemnella*) *longissima* Schulz, 1979

1979. *Belemnella* (*Bln.*) *longissima* Schulz, p. 98, pl. 2, figs 1–9, pl. 12, fig. 6, text-fig. 55 (with additional synonymy).
2007. *Belemnella inflata* (Archangielski, 1912); Remin, p. 117 (*pars*), pl. 7, fig. 7, *non* pl. 7, figs 1–6, 8.
2012. *Belemnella inflata* (Archangielski, 1912); Remin, p. 524 (*pars*), pl. 7, fig. 7, *non* pl. 7, figs 1–6, 8.

HOLOTYPE: KK408 (= SGPIH 2068), the original of Schulz (1979, pl. 2, figs 3–4; pl. 12, fig. 6), from 7.1 m above the base of the *lanceolata* Zone at the quarry 'Saturn' (Kronsmoor), by original designation.

MATERIAL: One specimen (ZI/65/Raj N/001) from Raj N, Solec Opoka.

DESCRIPTION: The guard is extraordinarily large, distinctly lanceolate in ventral and slightly lanceolate in lateral view. SD, AA and FA are very small (Table 4).

Vascular markings are weakly developed, but longitudinal striae are visible. Together with the vascular markings they form a pseudogranulate sculpture on the surface of the guard. The range of variation of Lsn *vs* AV is shown in Text-fig. 5.

	ZI/65/Raj N/001
Ls [mm]	87.0
Dp [mm]	13.6
Lsn [mm]	86.8
AV [%]	40.8
AL [%]	26.5
SD [mm]	0.0
AA [°]	11
FA [°]	11

Table 4. Measurements of critical characters of *Belemnella longissima* from the Solec Opoka

DISCUSSION: *Belemnella longissima* differs from congeners by its greater standardised length (Lsn > 82 mm), in combination with a rather lanceolate shape in ventral view (AV > 30 %). At Kronsmoor, it is especially common in the middle portion of the *lanceolata* Zone, 4–8 m above its base. The specimen from Raj N stems from the same stratigraphic interval. Remin (2007, 2012) referred this specimen to *Bln. inflata*.

DISTRIBUTION: Schulz (1979) recorded *Bln. longissima* from the uppermost Campanian *lanceolata* Zone to the Lower Maastrichtian lower *sumensis* Zone at Kronsmoor. It is also known from the Dnjepr-Donets basin (Nikitin 1958) and the Middle Vistula River Valley section.

Subgenus *Pachybelemnella* Schulz, 1979

Belemnella (*Pachybelemnella*) *inflata* (Arkhangelsky, 1912)

1912. *Belemnitella lanceolata* Schlotheim var. *inflata*; Arkhangelsky, p. 609, pl. 9, figs 4, 6, 10–11, ?27; pl.10, fig. 12.

1979. *Belemnella* (*P.*) *inflata* (Archangelsky, 1912); Schulz, p. 107, pl. 6, figs 1–10, text-fig. 59 (with additional synonymy).

1988. *Belemnella* (*P.*) *inflata* (Arkhangelsky, 1912); Christensen, p. 80, pl. 1, figs 1–6, ?7.

2007. *Belemnella* sp. A; Remin, p. 101 (*pars*), pl. 2, figs 1–8.

2007. *Belemnella longissima* Schulz, 1979; Remin, p. 108 (*pars*), pl. 1, figs 3, 6, 8, *non* pl. 1, figs 1–2, 4–5, 7, 9–10.

2007. *Belemnella lanceolata* (Schlotheim, 1813); Remin, p. 116 (*pars*), pl. 6, figs 2, 4, ?6, 7, 8, 10, 11, *non* pl. 6, figs 1, 3, 5, 9.

2007. *Belemnella inflata* (Archangielski, 1912); Remin, p. 117 (*pars*), pl. 7, figs 1–6, 8, *non* pl. 7, fig. 7.

2010. *Belemnella* (*Pachybelemnella*) cf. *inflata* (Arkhangelsky, 1912); Keutgen *et al.*, p. 117, fig. 11F–K.

2012a. *Belemnella* (*Pachybelemnella*) *inflata* (Arkhangelsky, 1912); Jagt, p. 131, fig. 28 O–P.

2012b. *Belemnella* (*Pachybelemnella*) cf. *inflata* (Arkhangelsky, 1912); Jagt, p. 99, pl. 1, figs 1–3.

2012. *Belemnella* sp. A; Remin, p. 518 (*pars*), pl. 2, figs 1–8.

2012. *Belemnella longissima* Schulz, 1979; Remin, p. 517 (*pars*), pl. 1, figs 3, 6, 8, *non* pl. 1, figs 1–2, 4–5, 7, 9–10.

2012. *Belemnella lanceolata* (Schlotheim, 1813); Remin, p. 522 (*pars*), pl. 6, figs 2, ?6, 7, 8, 10, 11, *non* pl. 6, figs 1, 3–5, 9.

2012. *Belemnella inflata* (Archangielski, 1912); Remin, p. 524 (*pars*), pl. 7, figs 1–6, 8, *non* pl. 7, fig. 7.

HOLOTYPE: A holotype for *Bln. inflata* has not yet been designated (Schulz 1979). Here, the population concept of this species as proposed by Schulz (1979, p. 108) is applied, to which reference is made for a detailed discussion.

MATERIAL: 11 specimens (ZI/65/Raj N/002, ZI/65/Raj N/009, ZI/65/Raj N/019, ZI/65/Raj N/022, ZI/65/Raj N/023, ZI/65/Raj N/027, ZI/65/Raj N/030, ZI/65/Raj N/032, ZI/65/Raj N/040, ZI/65/Raj N/051, ZI/65/Raj N/060) from Raj N; three specimens (ZI/65/Kłudz N/003, ZI/65/Kłudz N/008, ZI/65/Kłudz N/009) from Kłudzie N, from the Solec Opoka.

DESCRIPTION: The guards range from small to extraordinarily large, most specimens being large to very large. The standardised length ranges from 60.5 to 74.7 mm. The shape of the guards is distinctly lanceolate in ventral and slightly lanceolate in lateral view, with AV ranging from 15.5 to 45.0% and AL ranging from 5.4 to 28.2%. SD varies between 0 and 1.5 mm, while AA range between 11° and 14° and FA between 12° and 41° (Table 5). Vascular markings are weakly developed. The range of variation of Lsn *vs* AV is shown in Text-figs 5–6.

	Bln. inflata (Raj N)	*Bln. inflata* (Kłudzie N)
Ls [mm]	67.7 ± 5.6 (n = 11)	61.8 ± 7.7 (n = 3)
Dp [mm]	12.1 ± 2.2 (n = 11)	9.8 ± 0.4 (n = 3)
Qp [—]	0.99 ± 0.03 (n = 11)	0.93 ± 0.05 (n = 3)
WQs [—]	1.5 (n = 1)	—
Lsn [mm]	70.1 ± 3.3 (n = 11)	68.6 ± 7.1 (n = 3)
AV [%]	31.9 ± 8.7 (n = 11)	25.2 ± 6.7 (n = 3)
AL [%]	16.1 ± 6.8 (n = 11)	9.0 ± 3.1 (n = 3)
SD [mm]	0.5 ± 0.7 (n = 11)	0.8 ± 0.8 (n = 3)
AA [°]	12.2 ± 1.1 (n = 10)	12.3 ± 0.6 (n = 3)
FA [°]	21.5 ± 8.5 (n = 11)	29.7 ± 2.3 (n = 3)

Table 5: Univariate analysis of *Belemnella inflata* from the Solec Opoka

DISCUSSION: With respect to the results from the univariate analysis, the specimens here referred to as *Bln. inflata* are similar to those reported by Schulz (1979). The specimens from Raj N resemble *Bln. inflata* f.a.1 from the lower and middle *lanceolata* Zone, but also those from the *vistulensis* (former *pseudobtusa*) Zone at Kronsmoor.

Of note are the small alveolar angles of *Bln. inflata* from the Middle Vistula River Valley section, which are smaller than those reported by Schulz (1979) and Christensen (1988). In comparison with *Bln. inflata* from Nagoryany (Ukraine), the specimens from the Middle Vistula River Valley section are also slightly more lanceolate in ventral view.

The Raj N section has yielded three specimens (ZI/65/Raj N/002, ZI/65/Raj N/027, ZI/65/Raj N/032) which are characterised by a rather lanceolate shape (AV between 41 and 45%) and slightly more slender guards (Lsn between 70 and 75 mm). They resemble *Bln. desnensis* as understood by Schulz (1979), who considered this species to have typical AV values of > 42% (p. 110) or > 44% (p. 50). At present, these individuals are considered extreme variants of *Bln. inflata*, but future studies may reveal that they should be referred to *Belemnella* (*P.*) *desnensis* (Jeletzky, 1941) *sensu* Schulz.

DISTRIBUTION: *Belemnella inflata* is widely distributed in the North European Province, in the latest Campanian *lanceolata* Zone and the earliest Maastrichtian *vistulensis* Zone.

Belemnella (*Pachybelemnella*) *vistulensis*
(Kongiel, 1962)
(Text-fig. 8)

1962. *Belemnitella gracilis vistulensis* Kongiel, p. 56, pl. 11, figs 10–12, ?*non* pl. 12, figs 4–6.
1979. *Belemnella* (*P.*) *pseudobtusa* Schulz, p. 112, pl. 8, figs 1–10, pl. 12, fig. 8, text-fig. 61.
2007. *Belemnella lanceolata* (Schlotheim, 1813); Remin, p. 116 (*pars*), pl. 6, figs 3, 9, *non* pl. 6, figs 1–2, 4–8, 10–11.
2007. *Belemnella* sp. I; Remin, p. 119 (*pars*), pl. 8, figs 3, 6–8, *non* pl. 8, figs 1–2, 4–5, 9–10.
2012. *Belemnella lanceolata* (Schlotheim, 1813); Remin, p. 522 (*pars*), pl. 6, figs 3, 9, *non* pl. 6, figs 1–2, 4–8, 10–11.
2012. *Belemnella vistulensis* (Kongiel, 1962); Remin, p. 525 (*pars*), pl. 8, figs 3, 6, 7, ?8, ?9, 11, ?12, *non* pl. 8, figs 1–2, 4–5, 10.

HOLOTYPE: The holotype (Mcd 190), by original designation, is the original of Kongiel (1962, pl. 11, figs 10–12) from Kłudzie (Middle Vistula River Valley section), currently in the collections of Muzeum Ziemi, Warsaw. It is refigured here (Text-fig. 8) and in Remin (2012).

Text-fig. 8. *Belemnella vistulensis* Kongiel, 1962; the holotype; A – ventral view; B – lateral view; C – lateral views of the ventrally split specimen; natural size

Measurements of the holotype (Mcd 190) of *Bln. vistulensis* by Z. Remin [terminology and methods follow Schulz (1979) and Christensen (1995, 1999)]: Ls = 46.60 mm, Bs = 8.09 mm, Bs = 8.67 mm, Bc = 8.17 mm, Ds = 7.76 mm, Dp = 8.83 mm, Dc = 8.66 mm, SD = 1.41 mm, AA = 17.9°, FA = 42.5°, Lsn = 55.0 mm, AV = –0.99%, AL = –10.23%, Qp = 0.982

Measurements of the paratype (Mcd 191) of *Bln. vistulensis* by Z. Remin [terminology and methods follow Schulz (1979) and Christensen (1995, 1999)]: Ls = 49.98 mm, Bs = 9.06 mm, Bs = 8.66 mm, Bc = 8.34 mm, Ds = 8.50 mm, Dp = 8.88 mm, Dc = 8.62 mm, SD = 1.90 mm, AA = 17.3°, FA = 54.9°, Lsn = 58.3 mm, AV = 8.26%, AL = –1.34%, Qp = 0.975

Measurements of the holotype (Mcd 190) of *Bln. vistulensis* by Z. Remin (terminology and methods in line with Remin 2012): LAP = 46.59 mm, LASVF = 47.24 mm, LAEVF = 51.13 mm, LABVF = 47.24 mm, SD = 1.40 mm, ND = 4.53 mm KD = 3.12, RDBSVF = 0.00 mm, MVD = 8.77 mm, DVDP = 8.82 mm, DVDEVF = 8.66 mm, VDP = 8.67 mm, VDEVF = 8.56 mm, AA = 17.86°, FA = 42.51°

Measurements of the paratype (Mcd 191) of *Bln. vistulensis* by Z. Remin (terminology and methods in line with Remin 2012): LAP = 49.97 mm, LASVF = 51.87 mm, LAEVF = 53.86 mm, LABVF = 51.87

mm, SD = 1.89 mm, ND = 3.88 mm KD = 1.99, RDBSVF = 0.00 mm, MVD = 9.09 mm, DVDP = 8.87 mm, DVDEVF = 8.98 mm, VDP = 8.65 mm, VDEVF = 8.45 mm, AA = 17.28°, FA = 54.94°

MATERIAL: From below the 'boundary marl': 4 specimens (ZI/65/Raj N/033, ZI/65/Raj N/050, ZI/65/Raj N/052, ZI/65/Raj N/071) from Raj N; one specimen (ZI/65/Kłudz N/001) from Kłudzie N; two specimens (ZI/65/Podole/001, ZI/65/Podole/016) from Podole. From above the 'boundary marl': 5 specimens (ZI/65/Podole/004, ZI/65/Podole/008, ZI/65/Podole/015, ZI/65/Podole/025, ZI/65/Podole/030) from Podole; three specimens (ZI/65/Kłudz S/001, ZI/65/Kłudz S/002, ZI/65/Kłudz S/005) from Kłudzie S.

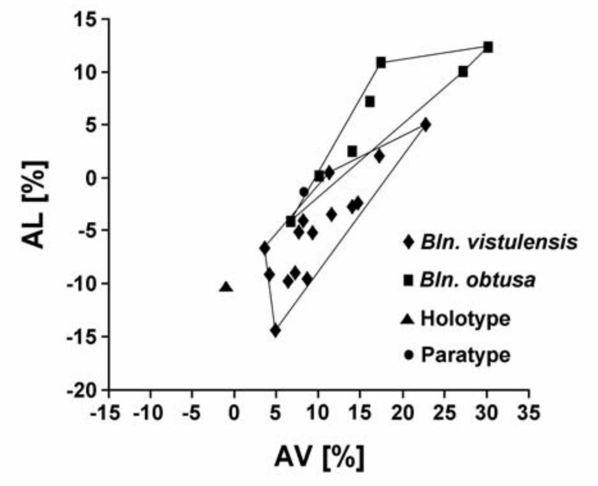
DESCRIPTION: The guards are small to large, most specimens being small. The shape of the guards is subcylindrical to slightly lanceolate in ventral view (AV between 3.5 and 22.7%) and subconical to subcylindrical in lateral view (AL between –14.4 to 5.0%). SD varies between 1 and 3.5 mm, while AA range between 13° and 18° and FA between 14° and 34° (Table 6). The guards are almost smooth, with the exception of dorsolateral double furrows. The ranges of variation of Lsn *vs* AV are shown in Text-figs 5–6. The two samples of *Bln. vistulensis* from below (Solec opoka) and above (Dziurków opoka) the 'boundary marl' do not differ significantly in any of the parameters listed in Table 6 (P > 0.45). Hence, stratigraphic forms of *Bln. vistulensis* cannot be distinguished in the material from the Middle Vistula River Valley section.

	Bln. vistulensis (Solec opoka)	*Bln. vistulensis* (Dziurków opoka)
Ls [mm]	53.1 ± 5.0 (n = 7)	52.0 ± 5.6 (n = 8)
Dp [mm]	11.9 ± 2.1 (n = 7)	11.2 ± 1.6 (n = 8)
Qp [—]	0.97 ± 0.03 (n = 7)	0.96 ± 0.03 (n = 8)
WQs [—]	2.3 (n = 1)	1.9 (n = 1)
Lsn [mm]	56.0 ± 2.4 (n = 7)	56.2 ± 4.5 (n = 8)
AV [%]	9.4 ± 4.7 (n = 7)	10.6 ± 6.0 (n = 8)
AL [%]	–5.1 ± 4.0 (n = 7)	–4.8 ± 6.1 (n = 8)
SD [mm]	2.2 ± 0.8 (n = 7)	2.4 ± 0.9 (n = 8)
AA [°]	16.1 ± 1.7 (n = 7)	16.0 ± 0.9 (n = 8)
FA [°]	23.3 ± 3.3 (n = 7)	21.4 ± 7.8 (n = 8)

Table 6. Univariate analysis of *Belemnella vistulensis* from the Solec and Dziurków opokas

DISCUSSION: *Belemnella vistulensis* differs from *Bln. inflata* in its smaller standardised length, less lanceolate shape, distinctly larger AA and slightly larger SD. The differences between *Bln. vistulensis* and *Bln. obtusa* are discussed below.

Kongiel (1962) erected a new subspecies, *Belemnitella gracilis vistulensis*, which he referred to the genus *Belemnitella*, because he did not accept the genus *Belemnella*. The holotype of his subspecies (pl. 11, figs 10–12; and Text-fig. 8 herein) is from Kłudzie, the paratype (pl. 12, figs 4–6) from Przedmieście Dalsze. While the holotype stems from the *Bln. vistulensis* Zone, the paratype may be from the lower *obtusa* Zone (Walaszczyk 2004; Remin *in* Niebuhr *et al.* 2011), although the presence of the topmost *vistulensis* Zone at Przedmieście Dalsze may not be excluded. From Kłudzie the following species have here been identified: *Bln.* cf. *lanceolata*, *Bln. inflata* and *Bln. vistulensis* (= *Bln. pseudobtusa sensu* Schulz). Kongiel's holotype of *Bln. vistulensis* differs from *Bln. lanceolata* and *Bln. inflata* in its lesser standardised length, distinctly subcylindrical shape in ventral and subconical shape in lateral views, as well as in its large AA. Text-fig. 9 compares the shape of the guards (AV *vs* AL) of *Bln. vistulensis* and *Bln obtusa* from the Middle Vistula River Valley section. Obviously, early representatives of *Bln. obtusa* are slightly more lanceolate in lateral view than specimens of *Bln. vistulensis*, but there is a considerable overlap. The holotype of *Bln. vistulensis* plots neither within the range of *Bln. vistulensis* (*Bln. pseudobtusa sensu* Schulz) nor within that of *Bln. obtusa*, but is closer to that of *Bln. vistulensis* (*Bln. pseudobtusa sensu* Schulz). With respect to its lateral aspect (AL), it matches the group of *Bln. vistulensis* (*Bln. pseudobtusa sensu* Schulz) well, but differs from that of *Bln. obtusa* from the Middle Vistula River Valley section. With respect to the ventral aspect, the holotype of *Bln. vistulensis* is more advanced (cylindrical) than the remaining material from the Middle Vistula River Valley section, but is within the documented range of *Bln. vistulensis* (= *Bln. pseudobtusa*) from Kronsmoor. With respect to the shape of the rostrum in ventral view the holotype of *Bln. vistulensis* is a fairly typical representative of *Bln. vistulensis* (*Bln. pseudobtusa sensu* Schulz), emphasising the slight difference in shape of *Bln. vistulensis* when compared to early forms of *Bln. obtusa*. The holotype of *Bln. vistulensis* must thus be placed into synonymy of *Bln. pseudobtusa sensu* Schulz, over which it has priority. The paratype of *Bln. vistulensis* plots within the overlap range of *Bln. vistulensis* and *Bln. obtusa* (Text-fig. 9). Based on its characters alone, at present it cannot be referred with confidence either to *Bln. vistulensis* or to *Bln. obtusa*.



Text-fig. 9. Relationship AV *vs* AL in *Bln. vistulensis* and *Bln. obtusa* from the Middle Vistula River Valley section, including data for the holotype and paratype of *Bln. vistulensis*.

DISTRIBUTION: *Belemnella vistulensis* is recorded from the Middle Vistula River Valley section, Kronsmoor and Norfolk (southeast England). It first appears in the latest Campanian and continues into the earliest Maastrichtian. The FAD of this species in the Middle Vistula River Valley section predates that in the Kronsmoor section.

Belemnella (*Pachybelemnella*) *obtusa* Schulz, 1979

1979. *Belemnella* (*P.*) *obtusa* Schulz, p. 114, pl. 9, figs 1–8, pl. 12, fig. 9, text-fig. 62.
1991. *Belemnella* (*Pachybelemnella*) *obtusa* Schulz, 1979; Keutgen and van der Tuuk, p. 18, pl. 3, figs 3–5.
1999. *Belemnella* (*P.*) *obtusa* Schulz, 1979; Christensen, p. 120, pl. 4, figs 26–32 (with additional synonymy).
2007. *Belemnella* sp. G; Remin, p. 112, pl. 3, figs 1–8.
2007. *Belemnella* sp. F; Remin, p. 113, pl. 4, figs 1–9.
2007. *Belemnella* sp. I; Remin, p. 119 (*pars*), pl. 8, figs 1, 5, 10, *non* pl. 8, figs 2–4, 6–9.
2007. *Belemnella obtusa* Schulz, 1979; Remin, p. 121 (*pars*), pl. 9, figs 1–6, ?8, 9, *non* pl. 9, fig. 7.
2012a. *Belemnella* (*Pachybelemnella*) *obtusa* Schulz, 1979; Jagt, p. 131, fig. 28 D.
2012b. *Belemnella* (*Pachybelemnella*) *obtusa* Schulz, 1979; Jagt, p. 100, pl. 3, figs 5–6, *non* pl. 3, figs 3–4.
2012. *Belemnella* sp. G; Remin, p. 519, pl. 3, figs 1–8.
2012. *Belemnella* sp. F; Remin, p. 520, pl. 4, figs 1–9.
2012. *Belemnella vistulensis* (Kongiel, 1962); Remin, p. 525 (*pars*), pl. 8, figs 1, 5, 10, *non* pl. 8, figs 2–4, 6, 7, ?8, ?9, 11, ?12.
2012. *Belemnella obtusa* Schulz, 1979; Remin, p. 527 (*pars*), pl. 9, figs 1–6, ?8, 9, *non* pl. 9, fig. 7.

HOLOTYPE: KN810 (= SGPIH 2123), the original of Schulz (1979, pl. 9, figs 3–4; pl. 12, fig. 9), from 24.4 m above the base of the *lanceolata* Zone in the quarry 'Saturn' (Kronsmoor), by original designation.

MATERIAL: 7 specimens (ZI/65/Dziu/004, ZI/65/Dziu/006, ZI/65/Dziu/010, ZI/65/Dziu/015, ZI/65/Dziu/016, ZI/65/Dziu/020, ZI/65/Dziu/023) from Dziurków, Dziurków Opoka.

DESCRIPTION: The rostra are large, with Ls varying between 55.4 and 65.2 mm. The shape of the guards is generally slightly lanceolate in ventral and subcylindrical to slightly lanceolate in lateral view (AV between 6.7 and 30.1%, AL between –4.2 to 12.4%). The SD ranges from 1.0 to 3.5 mm, the AA from 14° to 17.5° and the FA from 11° to 24° (Table 7). The surface of the guards is generally smooth or with weakly developed vascular markings. The range of variation of Lsn *vs* AV is shown in Text-fig. 10.

Bln. obtusa	
Ls [mm]	58.0 ± 3.5 (n = 7)
Dp [mm]	14.0 ± 1.5 (n = 7)
Qp [—]	1.00 ± 0.02 (n = 7)
WQs [—]	1.7 ± 0.6 (n = 4)
Lsn [mm]	57.1 ± 2.1 (n = 7)
AV [%]	17.4 ± 8.5 (n = 7)
AL [%]	5.6 ± 6.2 (n = 7)
SD [mm]	2.1 ± 1.0 (n = 7)
AA [°]	15.5 ± 1.6 (n = 7)
FA [°]	18.1 ± 5.0 (n = 7)

Table 7. Univariate analysis of *Belemnella obtusa* from the Dziurków Opoka

DISCUSSION: *Belemnella obtusa* differs from *Bln. inflata* in its lesser standardised length, less lanceolate shape, distinctly larger AA and larger SD. It is near-homeomorphic with *Bln. vistulensis* and single specimens are almost indistinguishable.

The sample of *Bln. obtusa* from the Dziurków Opoka differs significantly from that of *Bln. vistulensis* (sub-samples from above and below the 'boundary marl' were lumped for the statistical analyses) with respect to the greater length of the guard (Ls; $P < 5\%$), the greater diameter at protoconch (Dp; $P < 1\%$) the more lanceolate shape in ventral (AV; $P < 5\%$) as well as in lateral view (AL; $P < 0.1\%$), and in the shape of the cross-section at protoconch (Qp; $P < 1\%$). According to Schulz (1979, p. 114), slight differences exist between *Bln. obtusa* and *Bln. vistulensis* in the ontogenetic development of the shape of the cross section at the protoconch. Since the guards of *Bln. obtusa* and *Bln. vistulensis* from the Middle Vistula River Valley section differ in size, the observed difference in the mean values of Qp by T-test must be considered with reservation. Stratigraphic forms of *Bln. vistulensis* could not be distinguished in the material from the Middle Vistula River Valley section and, hence, the observation of Schulz (1979) that especially the late form of *Bln. pseudobtusa* (i.e., *Bln. vistulensis*) differed from *Bln. obtusa* in their smaller values for AL and larger SD could not be confirmed. Nevertheless, the highly significant difference ($P < 0.1\%$) for AL between early forms of *Bln. obtusa* and *Bln. vistulensis* from the Middle Vistula River Valley section is emphasized here for separating the two species.

When compared to *Bln. vistulensis* from the Middle Vistula River Valley section, *Bln. obtusa* from Dziurków is also less advanced with respect to the more lanceolate shape of the guards in ventral view (AV; $P < 5\%$). This difference does not represent a specific characteristic separating both taxa, although it is typical of the boundary interval close to the base of the *obtusa* Zone. Schulz (1979) interpreted this change as follows: *Bln. pseudobtusa* (i.e., *Bln. vistulensis*) became extinct slightly below the top of the *pseudobtusa* (i.e., *vistulensis*) Zone, while (a) population(s) of *Bln. inflata* rapidly transformed to a species resembling *Bln. vistulensis*, viz. to *Bln. obtusa*. The earliest representatives of *Bln. obtusa* thus resemble their ancestor, *Bln. inflata*, in their more lanceolate shape.

There is evidence that the dorsoventral diameter at protoconch (Dp) in *Bln. obtusa* is generally greater than in *Bln. vistulensis*: the mean value of Dp of *Bln. vistulensis* is 11.5 mm in the Middle Vistula River Valley section (maximum value observed: 15.1 mm), that of *Bln. obtusa* 14.0 mm (maximum value 16.9 mm). For comparison, the means for Kronsmoor are 10.4 and 10.9 mm for early and late forms of *Bln. pseudobtusa* (i.e., *vistulensis*), respectively (maximum value observed: c. 16.0 mm), whereas the means of *Bln. obtusa* range between 14.0 and 14.7 mm from early to late forms (maximum value: c. 18.7 mm) (Schulz 1979, table 2). It is concluded that *Bln. vistulensis* was a smaller species than *Bln. obtusa*.

Schulz (1979) distinguished early, middle and late forms of *Bln. obtusa*. Early forms are characterised by mean AV values of populations between 10–20% and Lsn between 54–60 mm, which is why the present sample is considered as an early form. In the lower *obtusa* Zone Schulz distinguished between two groups ("Schichtgruppenfaunen"). The group collected from 15–18 m above the base of the *lanceolata* Zone is characterised by the presence of AV values in excess of 20%, while that collected from 18–21 m above the base of the *lanceolata* Zone typically comprises specimens with Lsn values < 50 mm. Specimens typical of the interval 15–18 m in Kronsmoor are present in the small sample from Dziurków, whereas those typical of the interval 18–21 m in Kronsmoor are lacking. The conclusion that *Bln. obtusa* from Dziurków indicates the level 15–18 m at Kronsmoor is well in line with the mean values of AV and Lsn, which fit best with the interval 15–17 m above the base of the *lanceolata* Zone (compare Schulz 1979, table 5).

DISTRIBUTION: *Belemnella obtusa* is recorded from Poland (Middle Vistula River Valley section), northern Germany (Kronsmoor, Zeltberg, Rügen), Denmark (Hvide Klint, Møns Klint), southeast England (Norfolk), the Netherlands (Beutenaken, Bovenste Bos) and southern Belgium (Mons Basin). It first appears in the early Maastrichtian and is the index species of the *obtusa* Taxon Range Zone.

Belemnella ex gr. *lanceolata*/*inflata*

2007. *Belemnella* sp. I; Remin, p. 119 (*pars*), pl. 8, fig. 9, *non* pl. 8, figs 1–8, 10.
2012. *Belemnella longissima* Schulz, 1979; Remin, p. 517 (*pars*), *non* pl. 1, figs 1–10.
2012. *Belemnella obtusa* Schulz, 1979; Remin, p. 527 (*pars*), *non* pl. 9, figs 1–9.

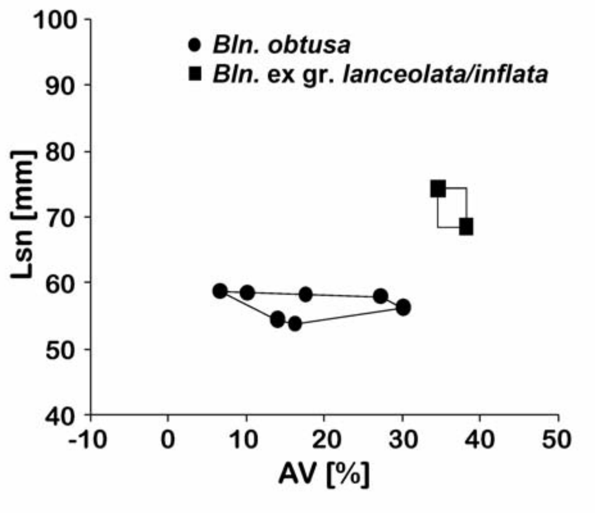
MATERIAL: 2 specimens (ZI/65/Dziu/001, ZI/65/Dziu/008) from Dziurków, Dziurków Opoka.

DESCRIPTION: The specimens are large to very large, distinctly lanceolate in ventral and slightly lanceolate in lateral view. The SD is close to nil, AA and FA are small (Table 8). Vascular markings are weakly developed or missing. The range of variation of Lsn *vs* AV is shown in Text-fig. 10.

	ZI/65/Dziu/001	ZI/65/Dziu/008
Ls [mm]	61.7	72.9
Dp [mm]	9.7	12.8
Lsn [mm]	68.5	74.3
AV [%]	37.9	34.6
AL [%]	24.3	20.8
SD [mm]	0.0	0.0
AA [°]	14	15
FA [°]	15	15

Table 8. Measurements of critical characters of *Bln*. ex gr. *lanceolata*/*inflata* from the Dziurków Opoka

DISCUSSION: Both specimens of *Bln*. ex gr. *lanceolata*/*inflata* fall within the range of variation of *Bln. lanceolata* from Balsvik, southern Sweden. However, the ranges of variation of *Bln. lanceolata* and *Bln. inflata* overlap considerably, so that the specimens mentioned here also plot within the range of variation of the latter, for example those from the Middle Vistula River Valley section. Schulz (1979) proposed that typical specimens of *Bln. lanceolata* usually were characterised by a standardised length (Lsn) in excess of 72 mm. ZI/65/Dziu/001 should thus be referred to *Bln*. *inflata*, whereas ZI/65/Dziu/008 would represent *Bln. lanceolata*. More horizontally collected material from Dziurków is needed to determine whether the specimens should be referred to *Bln. inflata* or to *Bln. lanceolata*.



Text-fig. 10. Relationship AV *vs* Lsn in *Bln*. *obtusa* and *Bln*. ex gr. *lanceolata*/*inflata* from the *obtusa* Zone of Dziurków, Dziurków Opoka

Belemnella sp.

2007. *Belemnella lanceolata* (Schlotheim, 1813); Remin, p. 116 (*pars*), pl. 6, fig. 6, *non* pl. 6, figs 1–5, 7–11.
2012. *Belemnella lanceolata* (Schlotheim, 1813); Remin, p. 522 (*pars*), pl. 6, fig. 6, *non* pl. 6, figs 1–5, 7–11.

MATERIAL: 2 specimens (ZI/65/Raj/081, ZI/65/Raj/082) from Raj, uppermost part of the Piotrawin Opoka.

DESCRIPTION: The fairly completely preserved specimen is large, slightly lanceolate in ventral and subcylindrical in lateral view. The values for SD, AA and FA are given in Table 9.

	ZI/65/Raj/081
Ls [mm]	59.1
Dp [mm]	11.5
Lsn [mm]	64.5
AV [%]	29.2
AL [%]	8.6
SD [mm]	1.6
AA [°]	15
FA [°]	19

Table 9. Measurements of critical characters of the complete specimen of *Belemnella* sp. from Raj

DISCUSSION: Remin (2007, 2008, 2012) referred both specimens of the genus *Belemnella* from Raj to *Bln. lanceolata*. However, Lsn of specimen ZI/65/Raj/081 is more typical of *Bln. inflata*.

In the Kronsmoor section, two groups of specimens may be distinguished in the lowermost 3 m of the *lanceolata* Zone, the first being typical of *Bln. inflata* and the second of *Bln. lanceolata*. According to Schulz (1979) it is uncertain with respect to the range of variation of *Bln. lanceolata* in Balsvik (southern Sweden), whether both groups of specimens should be united and referred to as *Bln. lanceolata*, or whether two species of *Belemnella*, viz. *Bln. lanceolata* and *Bln. inflata*, already co-occur at the basis of the *lanceolata* Zone in Kronsmoor.

With only one fairly complete specimen from Raj at hand, it is impossible to decide, whether *Bln*. (*Bln*.) *lanceolata* or *Bln*. (*P*.) *inflata sensu* Schulz (1979) is present. Consequently, both specimens are here referred to as *Belemnella* sp. However, since Lsn and AV of specimen ZI/65/Raj/081, one of the first representatives of the genus *Belemnella* in the Middle Vistula River Valley section, are within the range of variation of *Belemnella* recorded from the lowermost 3 m of the *lanceolata* Zone at Kronsmoor, it may be considered justified to refer them to *Bln. lanceolata* as proposed by Remin (2007, 2008, 2012) and, hence, to identify the basis of the *lanceolata* Zone in the Raj quarry.

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