

The *Belemnella* stratigraphy of the Campanian–Maastrichtian boundary; a new methodological and taxonomic approach

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ABSTRACT:

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The taxonomy and stratigraphy of the Upper Campanian and Lower Maastrichtian belemnites from the Vistula (central Poland) and Krons Moor (northern Germany) sections are revised on the basis of new collections from the Vistula section as well as a reinvestigation of the classic collection of Schulz from the Krons Moor section. For the taxonomic description a new biometric procedure is proposed, which can be applied to both the genera *Belemnella* and *Belemnitella*. For the species-level taxa recognition the Artificial Neural Networks method, the self-organizing Kohonen algorithm, was implemented. This new taxonomic and methodological approach enabled the recognition of nine species of the genus *Belemnella*. Five of them can be assigned to the existing species *B. lanceolata*, *B. longissima*, *B. inflata*, *B. obtusa* and *B. vistulensis*. However, the species concept differs from that applied by Schulz (1979). As a consequence, the stratigraphic ranges of these species are modified. Four species are left in open nomenclature and represent possibly new species. Future studies may reveal that they might be assigned to East European forms from Ukraine or Russia.

The species of *Belemnella* recognized are placed into the stratigraphic framework based on the standard ammonite and inoceramid bivalve zonations, especially those recognized in the Vistula section. The newly proposed belemnite zonation for the Vistula and Krons Moor sections is correlated *via* inoceramids with the standard GSSP at Tercis, France, in order to identify the base of the Maastrichtian Stage. The Campanian–Maastrichtian boundary as defined in Tercis is placed here at the base of the newly defined *B. obtusa* and *B. vistulensis* Zones [“*obtusa/vistulensis*”] – thus it is markedly higher than the traditional boundary based on the FAD of representatives of the genus *Belemnella*. This new boundary coincides well with a distinct turnover of belemnite guard morphology and represents one of the most important points in the early evolutionary history of *Belemnella*.

Three belemnite zones defined by their lower boundaries are recognized in the Campanian–Maastrichtian interval, in addition to three subzones recognized within the *B. obtusa* Superzone. The *B. lanceolata* and *B. inflata* zones as understood here are referred to the Upper Campanian [Tercis definition]. The *B. obtusa* Zone is subdivided into three subzones, viz.: *Belemnella vistulensis*, *Belemnella* sp. G and *Belemnella* sp. F, which are referred to the Lower Maastrichtian [Tercis definition].

The fast evolving species of *Belemnella* enable the proposal of a biostratigraphic scheme with a resolution that is higher than those based on inoceramid bivalves and ammonites – the longevity of a belemnite zone could be as low as 200Ky.

Key words: Campanian; Maastrichtian; Vistula section; Krons Moor section; Belemnites; Biostratigraphy; Artificial Neural Networks; Campanian–Maastrichtian boundary.

INTRODUCTION

Belemnites are one of the critical fossil groups for the biostratigraphy of the Upper Campanian and Lower Maastrichtian of the Vistula section in central Poland. However, since Kongiel's (1962) monograph of belemnites from the Vistula section, no further study was undertaken, albeit the need of such studies was commonly recognized. The present analysis is based on a new integrated biometrical and methodological approach using Artificial Neural Networks, more precisely, the self-organizing Kohonen algorithm (compare e.g. Kohonen 1982; Haykin 1994; Patterson 1996; StatSoft 2006). This powerful method is commonly used to solve different kinds of classification problems and was successfully applied to species-level taxonomic recognition in belemnites (Remin 2007, 2008, 2009), as well as in Palaeozoic corals (Wrzolek and Remin 2009). The present paper provides a taxonomic description, illustrations and stratigraphic interpretation of the latest Campanian and earliest Maastrichtian belemnites of the genus *Belemnella* from the Vistula section. To test the usefulness of the Artificial Neural Network and calibrate the new results against the traditional *Belemnella* zonal scheme established by Schulz (1979) on material he collected from the Krons Moor section in northern Germany, the Schulz collection was analysed parallelly to a new collection from the Vistula section and the results were used to interpret the Vistula belemnites. The new belemnite scheme worked out herein is directly correlated with other biostratigraphic zonations, especially those based on ammonites and inoceramid bivalves.

The Campanian–Maastrichtian boundary interval in the Vistula section is one of the few, if not the only succession in Europe that has yielded all of the stratigraphically important macro- and microfossils. The interval studied is relatively well accessible and its palaeontological content is rich and diverse. Besides belemnites (investigated by Kongiel 1962), it has yielded rich assemblages of ammonites (Błaszkiwicz 1980; Kennedy *et al.* 1992; Machalski 2012), non-cephalopod molluscs (Abdel-Gawad 1986), inoceramid bivalves (Walaszczyk 2004), foraminifera (Peryt 1980, 2000) and nannofossils (Gaździcka 1978 and Burnett *et al.* 1992).

The importance of the Vistula section has markedly increased following the approval of the Tercis section, France, in 2001 as the GSSP for the Campanian–Maastrichtian boundary (Odin 2001; Odin and Laumurelle 2001). Although the Tercis section has a very good faunal record, it lacks belemnites, the traditional standard marker of the base of the Maastrichtian stage in Europe.

The Krons Moor section (northern Germany), another section with high potential as the boundary reference section, has a very good ammonite and belemnite record but does not yield inoceramids, which have recently appeared to be a very useful tool for long-distance correlation at least within the Euramerican biogeographic region (Walaszczyk *et al.* 2002; Odin and Walaszczyk 2003).

GEOLOGICAL SETTING, BELEMNITE SUCCESSION AND THE MATERIAL STUDIED

The material studied herein comes from the Middle Vistula section, in central Poland, and from the Krons Moor section, in northern Germany. The Polish section was recently characterized by Walaszczyk (2004, 2012, this issue) and details of the German section were documented by Schulz (1979) and Niebuhr *et al.* (2011). Consequently, only short summary descriptions of both sections are presented below.

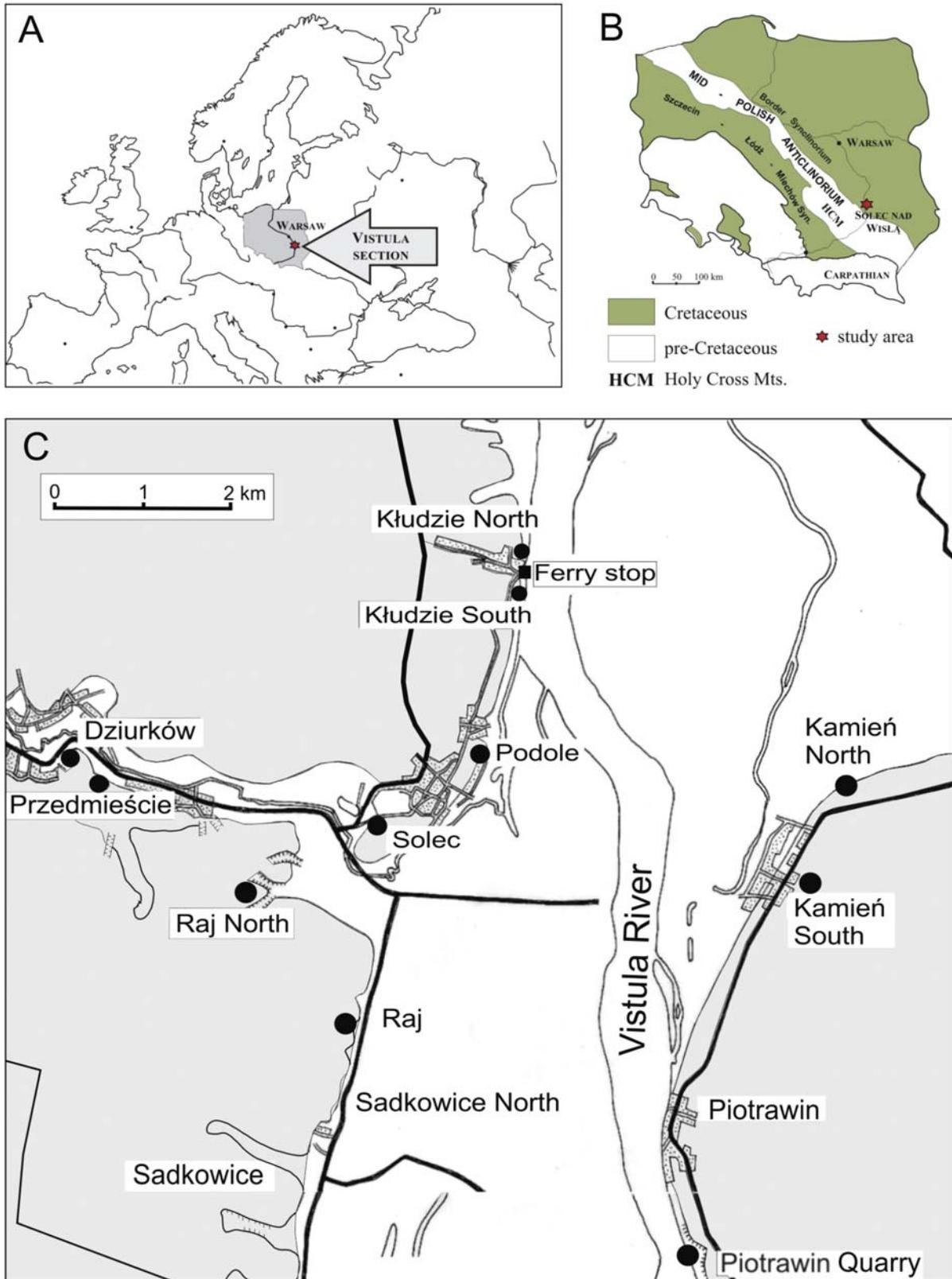
Middle Vistula Valley section

The part of the Middle Vistula Valley section containing *Belemnella* is well exposed on the western bank of the river, between the villages of Raj, Kłudzie, and Dziurków (Text-fig. 1), in a series of natural and artificial exposures. The sections on the eastern bank of the river, in the village of Kamień, mentioned in Kongiel (1962) and Błaszkiwicz (1980), are no longer available.

The Cretaceous succession of the Middle Vistula section forms a regular homocline, with a gentle dip (0°–10°) to NE (Text-fig. 1). Its topmost Campanian–lowermost Maastrichtian part is composed of monotonous, white to grey opoka, representing three of the five informal lithostratigraphic units of Walaszczyk (2004); in ascending order, the Piotrawin, Solec and Dziurków opokas (see Text-figs 2).

The genus *Belemnella* first appears in the topmost part of the Raj section (Text-figs 1, 2), c. 6 m above its base. The section, representing the topmost part of the Piotrawin Opoka, has so far yielded only one complete and one incomplete specimen with the alveolar portion preserved; these are undoubtedly assignable to the genus *Belemnella*, specifically to *Belemnella lanceolata* (Schlotheim, 1813).

Higher up, following a small observational gap, presumably a couple of metres (more in Walaszczyk 2004), the succession is exposed in the Raj North quarry (Text-figs 1, 2), represented by the Solec Opoka. Belemnites are common in this section and are dominated by the genus *Belemnella*, represented by (Text-fig. 3): *Belem-*



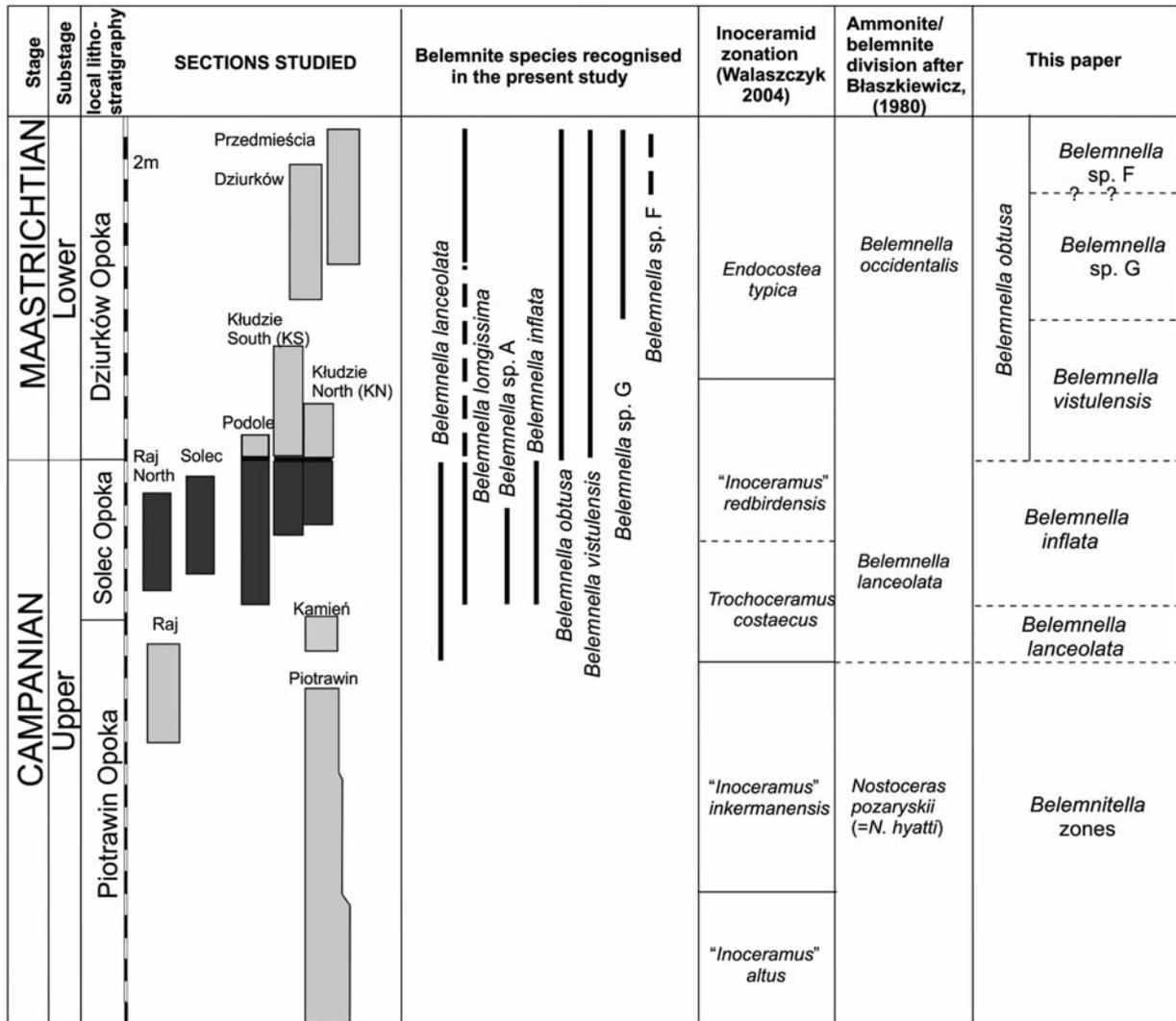
Text-fig. 1. A – location of the Vistula and Kronsmoor sections in Europe; B – Upper Cretaceous deposits in extra-Carpathian Poland. C – Locality map of the Upper Campanian through the Lower Maastrichtian in the Middle Vistula Valley section, central Poland (after Walaszczyk 2012)

nella lanceolata (Schlotheim, 1813), *Belemnella longissima* Schulz, 1979, *Belemnella inflata* (Arkhangelsky, 1912) and *Belemnella* sp. A. In inoceramid bivalve terms, this section represents the boundary interval between the *Trochoceras costaecus* and "*Inoceramus*" *redbirdensis* zones (Text-fig. 2) of Walaszczyk (2004, 2012).

Stratigraphically a little bit younger, but still within the "*Inoceramus*" *redbirdensis* Zone, is the succession of the Solec Opoka exposed in the Solec section (Walaszczyk 2004; and Text-fig. 2). The belemnites in this section are represented by the same forms as in Raj North (Text-fig. 2).

The highest part of the Solec Opoka and the basal part of the succeeding Dziurków Opoka are exposed in the Podole, Kłudzie South and Kłudzie North sections,

the stratigraphic ranges of which overlap to a considerable extent (Text-figs 1, 2). Within all of these sections a characteristic lithologic unit, the "boundary marl", marks the level taken as the boundary between the Solec and Dziurków opokas (Walaszczyk 2004; Text-fig. 2). The boundary marl enables a precise correlation of these three sections. Belemnites in the upper part of the Solec Opoka are quite common and are represented almost exclusively by *Belemnella*. Within the "boundary marl" as well as directly below and above this level, belemnites are rare or absent (Text-fig. 2). The belemnites below the "boundary marl" seem to represent exclusively species appearing already in the Raj North and Solec sections. A new assemblage appears above the "boundary marl", characterized by *Belemnella obtusa* and *B. vistulensis* (Text-fig. 2).



Text-fig. 2. Stratigraphic ranges of belemnite species and proposed belemnite zonation for the Middle Vistula Valley section, central Poland; inoceramid zones after Walaszczyk (2004); cephalopod zones after Błaszczewicz (1980); base of the Maastrichtian Stage according to (1) the GSSP in Tercis, France; (2) the conventional subdivision for the Boreal Realm, based on belemnites

The “boundary marl” seems thus to represent an interval in which one of the most important event in the early evolutionary history of *Belemnella* took place.

The topmost part of the succession studied, represented by the Dziurków Opoka, is exposed in the quarries of Dziurków and Przedmieścia, located west of the Vistula valley (Text-figs 1, 2). In both localities, the belemnites are represented by *Belemnella obtusa*, *Belemnella vistulensis* and *Belemnella* sp. G. Additionally, a single, albeit incomplete, specimen of *Belemnella* sp. F (Text-fig. 2) is known from Dziurków. Both sections also yielded a few specimens of *Belemnitella*.

The Przedmieścia and Dziurków sections belong to the lower part of the *Endocostea typica* inoceramid Zone (Walaszczyk 2004). According to Walaszczyk (2004), these sections represent the youngest strata available in the study area.

The succession studied yielded 75, more or less complete guards of the genus *Belemnella*, which formed the basis of the present analysis. The older material, of Pożaryski, Błaszkiwicz and, above all, of Kongiel, including the collection that he published in his monograph of 1962, could not be used, mainly due to the imprecise location of their specimens. All these collections are housed in the Museum of the Earth, Warsaw, and in the Museum of the Polish Geological Survey, in Warsaw.

Kronsmoor section

The Kronsmoor quarry is one of the few localities in northern Germany (Text-fig. 1A), where late Late Cretaceous rocks occur and it is the only place where the traditional Campanian–Maastrichtian boundary based on belemnites is exposed (Schulz 1978, 1979; Schmidt 1982; Niebuhr 2003, 2004; Niebuhr *et al.* 2011). The Campanian–Maastrichtian sequence is composed of white chalk with marly intercalations. A 100 m-thick sequence exposes an interval from the *Belemnitella langei* Zone *sensu* Schulz (1978) of the Upper Campanian up to the *Belemnella sumensis* Zone of the Lower Maastrichtian (e.g. Niebuhr 2003; Niebuhr *et al.* 2011). The sedimentation rate calculated for the Kronsmoor succession was estimated as about 24–25 m/million years (Ehrmann 1986; Niebuhr 2006; Voigt and Schönfeld 2010).

The traditional base of the Maastrichtian stage in the Kronsmoor section, marked by the FAD of *Belemnella lanceolata*, is taken at the flint layer bed F600 (Schulz 1979). The Campanian–Maastrichtian boundary as defined in Tercis was correlated with a level within the *Belemnella pseudobtusa* Zone *sensu* Schulz (1979) (Niebuhr 2003; Text-fig. 3). Based on the newly recog-

nized belemnite succession (Remin 2007, 2009; compare also Remin in Niebuhr *et al.* 2011), this boundary is placed at the level F600 + 10 m in Kronsmoor. It is the mid point between the last *B. inflata* and first *B. obtusa* as understood herein, within the two metre-thick interval, where belemnites are extremely rare or not present at all (Text-fig. 3).

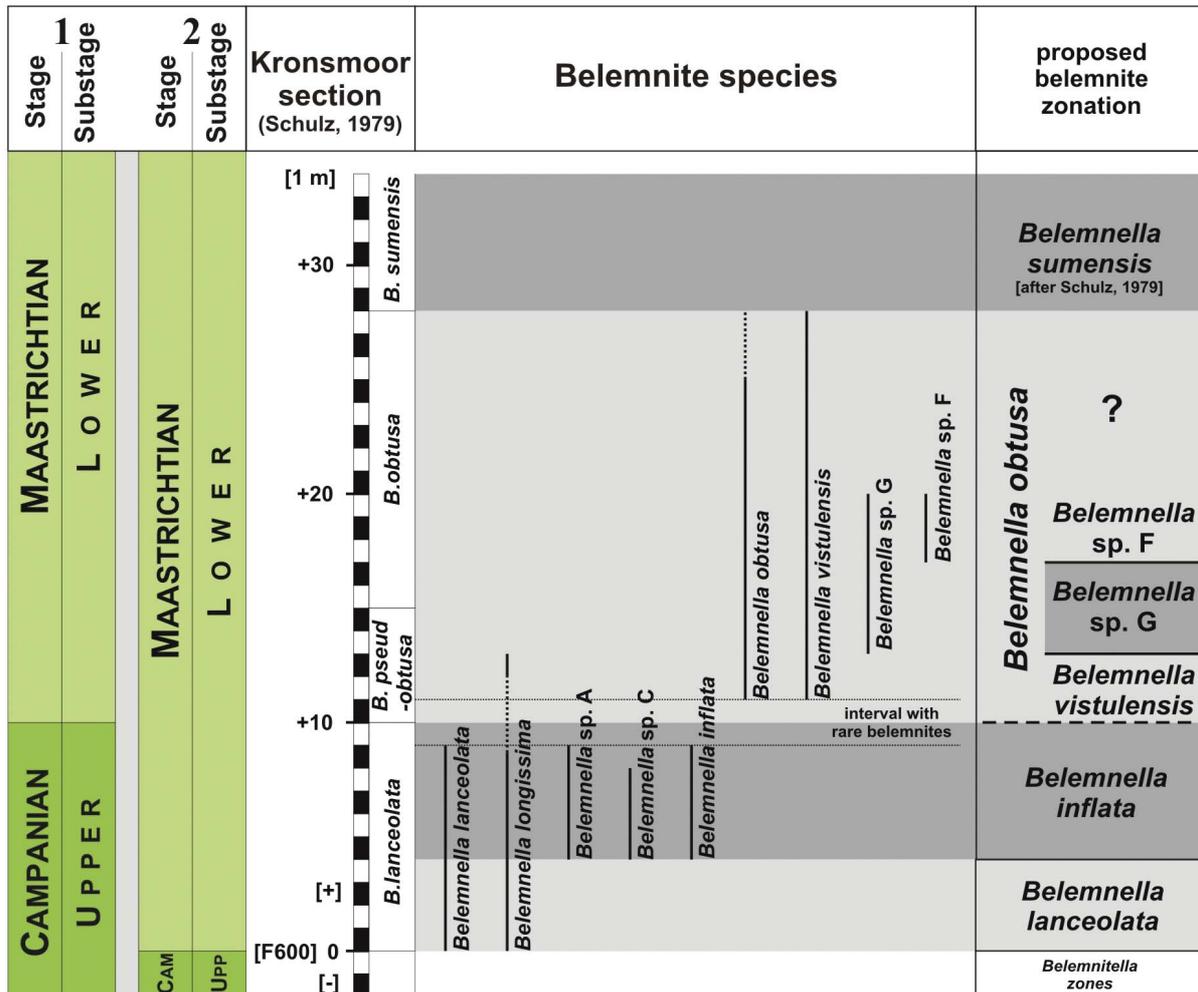
Level F600 of the Kronsmoor section is characterized by the entry of representatives of the genus *Belemnella*. Two species, *Belemnella lanceolata* and *Belemnella longissima*, enter almost simultaneously in Kronsmoor, at or just above this level (Text-fig. 3). In the 4 m-thick interval which follows [+0 m – +4 m], these are the only species of the genus *Belemnella* that occur. Higher up, representatives of *Belemnella* become more common and diverse. In the between +4 m and +9 m, five species are present: besides *Belemnella lanceolata* and *Belemnella longissima*, known also from below, appear *B. inflata*, *Belemnella* sp. A and *Belemnella* sp. C.

Belemnites almost disappear in the interval between +9 m and +11 m (Text-fig. 3). In the collection of Schulz, there are only three unidentifiable scraps of incomplete specimens from this interval. The belemnite assemblage that follows is quite different (Text-fig. 3). It is composed of *Belemnella obtusa* and *Belemnella vistulensis*, which enter the succession almost simultaneously at +11 m. They become successively more common higher up in the succession [in the interval between +16 m and +20 m]. At +13 m and +17 m, two new species appear, *Belemnella* sp. G and *Belemnella* sp. F, respectively (Text-fig. 3). From the interval between +21 m and the base of the *B. sumensis* Zone *sensu* Schulz (1979) at +28 m, there are only 3 specimens available for study.

BIOSTRATIGRAPHY

Traditionally, the base of the Maastrichtian stage in Europe was defined by the FAD of *Belemnella lanceolata* (Schlotheim 1813). The new proposal of the boundary, at the FAD of the ammonite *Pachydiscus neubergicus* (Hauer 1858), was provisionally accepted during the Brussels Symposium in 1995 (Odin 1996).

In 2001, the International Commission on Stratigraphy formally accepted the section at Tercis les Bains (near Dax, Landes, SW France) as the GSSP of the Campanian–Maastrichtian boundary (Odin 2001; Odin and Laumurelle 2001). The boundary is placed at the level 115.2 m of the Tercis quarry, and defined as an arithmetic mean of twelve bioevents (Odin and Laumurelle 2001): (1) FAD of the ammonite *Pachydiscus*



Text-fig. 3. Stratigraphic ranges of belemnite species and proposed belemnite zonation for the Kronsmoor section, northern Germany; base of the Maastrichtian Stage according to (1) the GSSP in Tercis, France; (2) the conventional subdivision for the Boreal Realm, based on belemnites. In the present paper, horizons above F600 are referred to in metres with [+]; the horizons below F600 are referred to in metres with [-]; the same scheme is applied in Niebuhr *et al.* 2011

neubergicus; (2) LO of the ammonite *Nostoceras hyatti*; (3) FAD of the ammonite *Didymoceras cylindraceum*; (4) LO of the dinoflagellate *Corradinisphaeridium horridum*; (5) LO of the dinoflagellate *Raetiaedinium truncigerum* [= *R. evittigratum*]; (6) LOs of the dinoflagellates *Samlandia mayii* and *S. carnarvonensis*; (7) FAD of the planktonic foraminifer *Contusotruncana contusa*; (8) FAD of the planktonic foraminifer *Rugoglobigerina scotti*; (9) FAD of the benthic foraminifer *Bolivinooides*; (10) LO of the benthic foraminifer *Gavelinella clemantina*; (11) FAD of species of the inoceramid genus *Trochoceras*; and (12) LO of the calcareous nannofossil *Quadrum trifidum*.

Despite a very good palaeontological record, the Tercis section lacks belemnites, which traditionally defined the Campanian–Maastrichtian boundary in Eu-

rope. The original assumption of near-equivalency of the base of the Maastrichtian as defined in Tercis with that defined by the FAD of *Belemnella lanceolata* (Christensen *et al.* 2000; Christensen 2001) was not confirmed by subsequent investigations (e.g. Niebuhr 2003; Walaszczyk 2004; Niebuhr *et al.* 2011).

Traditional *Belemnella* zonation

The genus *Belemnella*, which appeared close to the base of the Maastrichtian, as traditionally defined, dominated the belemnite record of the Early Maastrichtian, almost completely replacing the genus *Belemnitella*, which was well represented in the Late Campanian. Consequently, the genus *Belemnella* became the basis of the Lower Maastrichtian zonal schemes.

Birkelund (1957) subdivided the Lower Maastrichtian [traditional (Boreal) definition.] into two belemnite zones: the *Belemnella lanceolata* Zone, of the lower Lower Maastrichtian, and the *Belemnella occidentalis* Zone, of the upper Lower Maastrichtian (Text-fig. 4). Subsequently, Schulz (1979) proposed a more detailed zonation, subdividing the substage into six *Belemnella* zones (Text-fig. 4): *Belemnella lanceolata*, *B. pseudobtusa*, *B. obtusa*, *B. sumensis*, *B. cimbrica* and *B. fastigata*. Schulz (1979) referred his newly recognised forms to two separate subgenera; more slender forms to the nominative subgenus *Belemnella* (*Belemnella*) Nowak, 1913, and the stout forms to the subgenus *Belemnella* (*Pachybelemnella*) Schulz, 1979.

On the East European Platform, the base of the Maastrichtian has usually been placed at the entrance level of *Belemnella licharewi* Jeletzky, 1941 (Text-fig. 4), the FAD of which seems to more or less correspond to the FAD of *B. lanceolata*. Schulz (1979) included *B. licharewi* into the synonymy of *Belemnella desnensis* Jeletzky, 1941, a species reported from the middle part of his *B. lanceolata* Zone in Krons Moor (Text-fig. 4).

The new zonation

The *Belemnella* record of the Vistula and Krons Moor sections forms the basis of the new zonation, pre-

sented herein. Three zones and three subzones are recognized (Text-figs 2, 3): *Belemnella lanceolata* Zone, *Belemnella inflata* Zone and *Belemnella obtusa* Zone; the latter subdivided into the subzones of *Belemnella vistulensis* (former *B. sp. I* in Remin in Niebuhr *et al.* 2011), *Belemnella sp. G* and *Belemnella sp. F*. All of the zones and subzones are defined as interval range zones. The correlation with the *Belemnella* zonation of Schulz is presented and discussed in the accompanying paper by Keutgen *et al.* (2012 this issue).

This new zonation is correlated against the inoceramid zonation, as recently recognized in the Vistula section by Walaszczyk (2004), which enables correlation of the the belemnite scheme with the stratotypic succession in Tercis, France (Walaszczyk *et al.* 2002a, b; Odin and Walaszczyk 2003) (Text-fig. 2). This correlation shows that the Campanian–Maastrichtian boundary as defined at Tercis corresponds to the basal part of the *Belemnella obtusa* Zone as understood herein. It is distinctly higher than the entry level of *Belemnella lanceolata*, which traditionally defined the base of the Maastrichtian stage in Europe (see also Niebuhr *et al.* 2011; compare Text-fig 2).

The *Belemnella lanceolata* Zone; uppermost Campanian. The base of this zone is defined by the FAD of the index taxon, and its top by the FAD of *Belemnella*

1		2		I proposed zones for the Vistula and Krons Moor sections	II NW Europe	III Russian Platform	IV Conventional zones
Stage	Substage	Stage	Substage				
MAASTRICHTIAN	LOWER	MAASTRICHTIAN	LOWER		<i>Belemnella fastigata</i>	<i>Belemnella sumensis</i>	<i>Belemnella occidentalis</i>
					<i>Belemnella cimbrica</i>		
				<i>Belemnella sumensis</i>			
CAM.	UPP.	MAASTRICHTIAN	LOWER	<i>Belemnella obtusa</i>	<i>Belemnella obtusa</i>	<i>Belemnella lanceolata</i>	<i>Belemnella lanceolata</i>
				no data			
				<i>Belemnella sp. F</i>	<i>Belemnella pseudobtusa</i>		
				<i>Belemnella sp. G</i>			
				<i>Belemnella inflata</i>	<i>Belemnella lanceolata</i>	<i>Belemnella licharewi</i>	
				<i>Belemnella vistulensis</i>			
				<i>Belemnella lanceolata</i>			

Text-fig. 4. The correlation of proposed belemnite zones; I – Middle Vistula Valley (central Poland) and Krons Moor (northern Germany) sections – this paper; II – NW Europe (Schulz, 1979); III – Russian Platform (Naidin 1975, 1979); IV – conventional belemnite zones (Birkelund 1957 in harmony with previous belemnite zonation of the Vistula section (Błazkiewicz 1980); base of Maastrichtian Stage according to (1) the GSSP in Tercis, France; (2) the conventional subdivision for the Boreal Realm, based on belemnites

inflata as understood herein. The zone corresponds approximately to the lower part of the *Trochoceramus costaeus* inoceramid Zone (Text-figs 2), and possibly to the uppermost part of the preceding “*Inoceramus*” *inkermanensis* Zone.

In the Vistula section, the base of the zone is exposed at the top of the Raj section and its upper boundary is located somewhere between the Raj and Raj N sections (Text-figs 1, 2).

In Krons Moor the *B. lanceolata* Zone, as defined herein, spans an interval from the level F600 [=0 m] up to +4 m, which is distinctly shorter than the *B. lanceolata* Zone *sensu* Schulz (1979) (compare Text-figs 3, 4).

The *Belemnella inflata* Zone; uppermost Campanian. The base of this zone is defined by the FAD of the index taxon, and its upper boundary by the FAD of *Belemnella obtusa*, as defined herein, or the entry of *B. vistulensis* (Text-figs 2, 3, 4). Five belemnite species were recognised in this zone (Text-fig. 2). It corresponds to the upper part of the *Trochoceramus costaeus* Zone and lower part of the “*Inoceramus*” *redbirdensis* Zone.

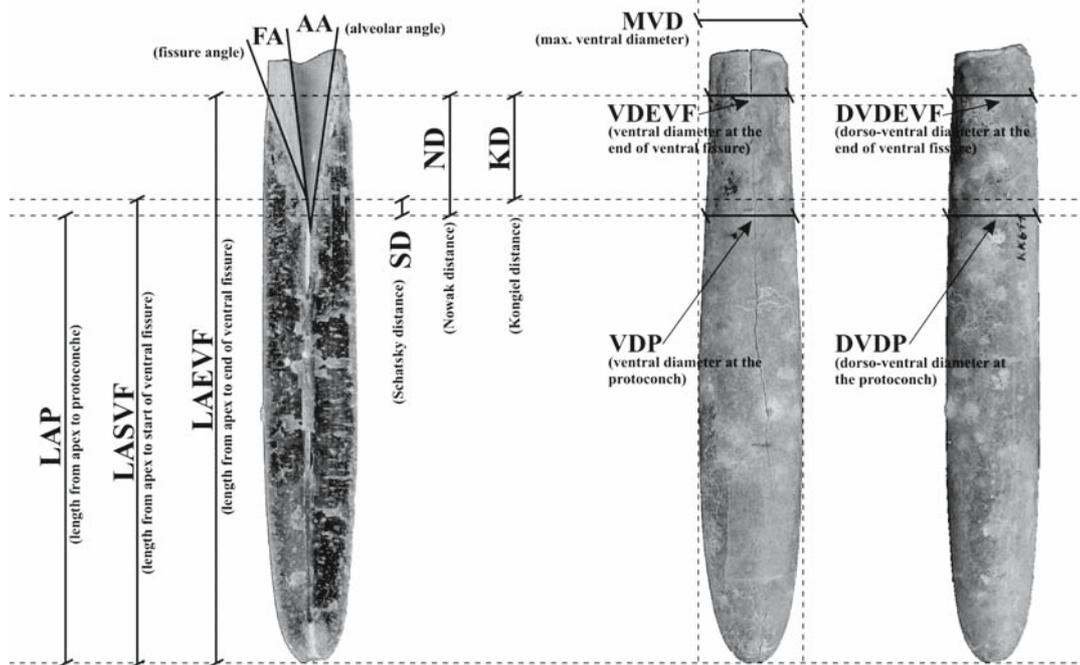
In the Vistula section, the lower boundary of this zone is not exposed. Its higher part is best exposed in the Raj N working quarry, but is also accessible in the Solec, Podole, Kłudzie S and Kłudzie N sections (Text-figs 1, 2). Its upper boundary seems to be close to the “boundary marl” (Text-fig. 2).

In Krons Moor, the *Belemnella inflata* Zone, as defined herein, comprises the interval from +4 m to +10 m, which corresponds to the upper six metres of the *lanceolata* Zone *sensu* Schulz (Text-figs 3, 4).

The *Belemnella obtusa* Zone; ?topmost Campanian to lowermost Maastrichtian. The FAD of the index taxon or the entry of *B. vistulensis*, which most probably coincide, defines the base of this zone. Its upper boundary is defined by the FAD of *B. sumensis sensu* Schulz. In inoceramid terms, the zone corresponds to the upper part of the “*Inoceramus*” *redbirdensis* Zone, *Endocostea typica* Zone and, most probably, part of the succeeding *Trochoceramus radiosus* Zone. The zone is subdivided into the *Belemnella vistulensis*, *Belemnella* sp. G and *Belemnella* sp. F subzones.

In the Vistula section, the base of the *obtusa* zone is placed immediately above the “boundary marl” exposed at Podole, Kłudzie S and Kłudzie N. Higher parts of the zone are exposed in the Dziurków and Przedmieścia sections (Text-figs 1, 2). Its upper boundary is not exposed. It seems that the “boundary marl” is the equivalent of the interval from +9 m to +11 m of the Krons Moor section, where belemnites are extremely rare (Text-fig. 3). The assemblages below and above this level differ significantly in both the Vistula and Krons Moor sections.

In Krons Moor, the highest record of *B. obtusa sensu* Schulz is at the +25 m level (Text-figs 3, 4). The *B. ob-*



Text-fig. 5. Terminology and measurements of external and internal features of the belemnite guard (Remin, 2007, 2008); two features not illustrated are: LABVF – length from apex to most posterior part of ventral fissure; RDBSVF – (= LASVF – LABVF), for details compare Remin (2007, 2008)

tusa Zone, as defined herein, corresponds to the *pseudobtusa* and *obtusa* zones *sensu* Schulz (1979), and comprises an interval from +10 m to +28 m (Text-fig 3).

The *B. obtusa* Zone is subdivided into three subzones, the *B. vistulensis*, *Belemnella* sp. G, and *Belemnella* sp. F subzones. All are defined as interval subzones. The subzones are well defined in the Kronsmoor section, where they span the intervals: +10 m to +13 m; +13 m to +17 m; and an interval above +17 m respectively (Text-fig 4). No precise subdivision is possible, however, in the Vistula section. The *Belemnella vistulensis* Subzone should span the topmost parts (above the “boundary marl”) of the Podole and Kłodzie sections. The two higher subzones definitely span a higher interval, comprised by the succession exposed in Przedmiescia and Dziurków. However, their boundaries cannot be precisely located; the accessible specimens are loose, rare finds (a single incomplete specimen in the case of *Belemnella* sp. F), and they do not allow for any reliable subdivision. Consequently, the boundary between the intervals of *Belemnella* sp. G and of species F is shown with a question mark (Text-fig 2).

THE BIOMETRIC PROCEDURE

The biometry and measurements of belemnite guards, as used herein, are slightly modified versions of the methods used by Kongiel (1962), Schulz (1979) and Christensen (1975). The measurement procedure is as follows:

1. Unsplit guards and both halves of split guards are photographed in ventral and dorso-ventral views.
2. The maximum length of the entire preserved guard and of both halves of the dorso-ventrally split guard are measured with a vernier caliper to a precision of 0.01 mm. The photographed guards are rescaled in graphic applications (e.g. Corel®) to their original size.
3. All other measurements are made on scaled photographs, which gives much higher precision than measurements made on the guard (Text-fig. 5).

Measured parameters

(LAP) length from the apex to the protoconch: measured from the base of mucro (without mucro) to the mid point of the protoconch (Text-fig. 5; compare Schulz 1979). As the mucro is very often broken, the measurement does not include it. The mid point of the protoconch is chosen to avoid errors – the front and back walls of the protoconch are often poorly preserved, whereas the oval shape of the protoconch is usually vis-

ible. Christensen (1973–2002) defined the LAP as the length from the apex to the anterior wall of the protoconch.

(LASVF) length from the apex to the start of the bottom of ventral fissure: measured from the apex (without mucro) (Text-fig. 5). Christensen (1975) described this length as LAVF, length from the apex to the ventral fissure, although he did not define it. He did not use it, considering it as a size-dependent parameter [like LAP, DVDP, SD, AA and FA].

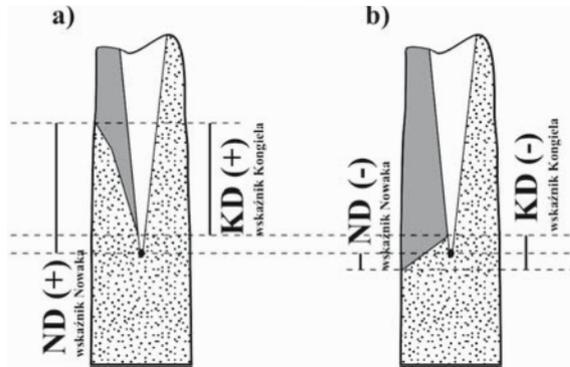
(LAEVF) length from the apex to the end of the bottom of ventral fissure: length measured from the apex (without mucro) to the intersection of the bottom of the ventral fissure and the outer surface of the guard (Text-fig. 5). This feature was proposed by Nowak (1913) and used by Kongiel (1962; pp. 7–8) as the *relative length of guard*.

(LABVF) length from the apex to the most posterior part of the bottom of the ventral fissure: new measurement. In most cases its value is equal to LASVF because, as a rule, the bottom of ventral fissure is swept forward. However, sometimes when the bottom of the ventral fissure is sinuously curved, it is initially swept back and then swept forward.

(RDBSVF) relative distance of the back of the bottom of ventral fissure: the distance to which the bottom of ventral fissure is swept back from its starting point on the alveolar wall (Text-fig. 5). This feature was introduced by Schulz (1979, p. 25) as *Schlitzboden-Amplitude*.

(SD) Schatsky Distance: the distance measured from the mid point of the protoconch to the starting point of the bottom of the ventral fissure on the alveolar wall (Text-fig. 5), measured parallel to the axis of the guard. The mid point of the protoconch is chosen for the reasons mentioned for LAP and to unify the measurements of ND, KD and RDBSVF. This definition follows that of Schulz (1979, p. 26), who termed this parameter the *Schatsky-Wert* (SW) [Schatsky value]. The SD was originally proposed by Jeletzky (1949a, p. 260) as the *Schatsky index* and defined as the distance between the anterior wall of the protoconch and the starting point of the bottom of the ventral fissure on the alveolar wall; the original definition was used by Birkelund (1957), Kongiel (1962) and Christensen (1973–2002).

(ND) Nowak Distance: the distance measured from the mid point of the protoconch to the intersection of the



Text-fig. 6. The internal structure of the guard and different position of the bottom of the ventral fissure; **a** – ND (+) and KD (+) are positive (+) when the outer end of the bottom of the ventral fissure is swept forward from the protoconch and from the inner end of the bottom of the ventral fissure respectively; **b** – ND (-) and KD (-) are negative (-) when the outer end of the bottom of the ventral fissure is swept back from the protoconch and from the inner end of the bottom of the ventral fissure respectively

bottom of the ventral fissure and the outer surface of the guard, measured parallel to the axis of the guard. Its value is positive (+) or negative (-), as illustrated in Text-fig. 6. This parameter was introduced by Kongiel (1962) as the *Nowak index*. Its definition, used herein, differs slightly from the original – the measurement starts at the mid point of the protoconch. Schulz (1979) and Christensen (1973–2002) did not use it as a size-dependent parameter.

(KD) Kongiel Distance: the distance between the starting point of the bottom of the ventral fissure on the alveolar wall and the intersection of the bottom of the ventral fissure with the outer surface of the guard, measured parallel to the axis of the guard. Its value is either positive (+) or negative (-), as illustrated in Text-fig. 6. This index was introduced by Kongiel (1962) as the *Fissure index*. It is re-named herein the Kongiel Distance in honour of Dr. Roman Kongiel.

(MVD) maximum ventral diameter: it is measured in ventral view (Text-fig. 5); based on photographs of whole guards.

(VDEVF) ventral diameter at the end of the ventral fissure: measured in ventral view at the end of the ventral fissure (Text-fig. 5); based on photographs of whole guards.

(VDP) ventral diameter at the (mid-point of) the protoconch: diameter measured in ventral view at the protoconch (Text-fig. 5); based on photographs of whole guards

(DVDEVF) dorso-ventral diameter at the end of the ventral fissure: diameter measured in dorso-ventral view (Text-fig. 5); based on photographs of whole guards.

(DVDP) dorso-ventral diameter at the (mid-point of) the protoconch: measured in dorso-ventral view (Text-fig. 5); based on photographs of whole guards.

(AA) alveolar angle: angle between the lines determined by the inner alveolar walls measured in dorso-ventral view (Text-fig. 5). Kongiel (1962) pointed out that the AA decreases slightly from the back to the front of the alveolus. Accordingly, Schulz (1979) measured the AA of the alveolar segment 10–20 mm from the protoconch. He also demonstrated that the differences in published AA values, based on different definitions of the parameter, were statistically significant.

(FA) fissure angle: angle between the alveolar wall and the line joining the starting point of the bottom of the ventral fissure on the alveolar wall and its end on the outer surface of the guard, measured in dorso-ventral view (Text-fig. 5). The definition of Skołodźrówna (1932), subsequently used by Kongiel (1962) and Christensen (1973–2002), is followed herein. Vassilienko and Rasmyslowa (1950) and Naidin (e.g. 1952) adopted a different definition. They described the FA as the angle between the alveolar axis and the line that joins the starting point and end points of the bottom of the ventral fissure. Schulz (1979) also proposed other angles connected with the trajectory of the bottom of ventral fissure (for definition of WS1, WS2 and WSm compare Schulz 1979, pp. 24–25), however, all of them are of minor significance. Their determination is very ambiguous – the bottom of the ventral fissure, its starting point and trajectory is very often invisible, what makes such measurements inconvenient or even impossible, resulting in a high degree of inaccuracy.

Ratios: The following ratios are used: SD/LAP; ND/LAP; SD/ND; SD/KD; KD/ND; LAP/LASVF; LAP/LAEVF; LASVF/LAEVF; VDP/DVDP; VDEVF/DVDEVF; VDP/MVD; VDEVF/VDP; DVDEVF/DVDP; DVDP/LAP.

Discussion of former biometric methods

This is an overview of biometric methods applied hitherto to the study of the genera *Belemnitella* d'Orbigny, 1840 and *Belemnella* Nowak, 1913. The older studies were broadly reviewed by Jeletzky (1946, 1949a, b, 1951a, b) and Naidin (1952), and only those relevant to

the group studied herein are briefly presented here. The methods of Kongiel (1962), Christensen (1975–2002) and Schulz (1979) are discussed in more detail.

Critical for the study of the genera *Belemnitella* and *Belemnella* was the publication of Nowak (1913). He was the first to take note of vascular imprints in belemnite taxonomy. He characterized the genus *Belemnitella* by an acute angle of the vascular imprints, which branch off from the dorso-lateral double furrows posteriorly at an angle of less than 30°. His new genus *Belemnella* was characterized by an obtuse angle of the vascular imprints (30°–90°). Nowak was the first worker to use biometry to differentiate between these two genera. The shape of the guard he described by coefficients of length, width, thickness and circumference.

In 1932, Skołozdrówna published on the taxonomic significance of the alveolus and ventral fissure. Analyzing c. 1000 specimens, she concluded that belemnite guards from four successive levels of the Upper Cretaceous of Poland could be characterized and distinguished by specific values of AA, FA and the shape of the bottom of ventral fissure.

Jeletzky (1946, 1948a, 1948b, 1948c, 1949a, 1949b, 1950, 1951a, 1951b, 1955, 1958) analyzed in detail a number of internal and external features, emphasizing or deprecate their taxonomic value. He generally considered that the internal features were taxonomically more important. In his 1949a paper he introduced the Schatsky Distance (SD; compare Text-fig. 5).

Vassilenko and Rasmyslowa (1950) questioned the validity of the genus *Belemnella*, synonymising it with the genus *Belemnitella*. They considered the FA, SD and the shape of the bottom of ventral fissure as taxonomically most important. Additionally, they introduced the concept of the *conditional length of guard*, defined as the length of the reconstructed guard (compare Kongiel 1962, p. 7).

In 1952, Naidin published a monographic description of belemnites from the western Ukraine. He based the taxonomic descriptions on several external and internal characters such as AA, FA, SD, the ratio of the alveolus depth to the length of the guard as well as the ratio of the length of the ventral fissure to the depth of the alveolus. Naidin, however, subjectively selected features considered by him as taxonomically more important and, as with Vassilenko and Rasmyslowa (1950) and Kongiel (1962), used the concept of the *reconstructed guard*.

The method of Kongiel

Kongiel, in his 1962 monograph of belemnites from the Middle Vistula valley, analysed 860 complete and

490 incomplete guards. Of these, 535 specimens are from the uppermost Maastrichtian (level “z” of Pożaryski 1938, 1948). In traditional belemnite zonal terms, 331 specimens came from the Upper Campanian–Lower Maastrichtian [67 from the lower Upper Campanian; 175 from the upper Upper Campanian and 89 from the Lower Maastrichtian]. Kongiel never accepted the genus *Belemnella* Nowak, 1913, and included all *Belemnella*-like guards in the genus *Belemnitella*.

Kongiel emphasized the importance of biometric methods, which he claimed to be the best way to get reliable results. He characterized the guards by several external and internal features (Kongiel 1962, pp. 7–9), for which the means, standard deviations and standard errors were calculated.

The main shortcoming of the methodology of Kongiel was an *a priori* subdivision of belemnite guards into separate species. Kongiel put special emphasis on ratio relationships in taxonomic recognition; however, three of the six ratios proposed by him (Kongiel 1962, pp. 8–9, 19) were based on a reconstruction of the anterior portion of the guard, to obtain the so-called conditional length of the guard (Kongiel 1962, fig. 1), and thus could be highly inaccurate.

The method of Christensen

Christensen (1975) proposed his own methodology for belemnite studies, emphasizing the need of biometry, mathematics and statistics, with particular reference to the statistical analysis of populations.

In descriptions of the genera *Belemnitella* and *Belemnella*, Christensen (1975) proposed several parameters. Most of them he regarded as functions of: LAP, DVDP, SD, FA and AA; consequently, all others, as well as ratios based on them, he regarded as of limited value (Christensen 1975, p. 31).

Christensen applied uni- and multivariate analyses, presenting the results as histograms, scatter-plots and regression lines. The relative growth of belemnites – isometric or allometric – he studied by regression analysis.

In 1995, Christensen introduced the *Birkelund Index* (BI), the ratio of the LAP [length from the apex to the anterior wall of the protoconch] and the DVDP [dorso-ventral diameter at the protoconch] and used this key ratio as the basis of species-level discrimination in the genus *Belemnitella*. This ratio was actually used earlier, and referred to as the *degree of elongation* by Birkelund (1957) or *elongation* by Schulz (1982) and by Keutgen and van der Tuuk (1990).

As with Kongiel, the main shortcoming of Christensen’s methodology was an *a priori* subdivision of belemnite rostra into separate species.

The method of Schulz

Schulz (1979) proposed a new methodology of species-level discrimination of the genus *Belemnella*. The results of his taxonomic studies and interpretations were expressed by a graphic diagram (Schulz 1979, fig. 53) for species-level taxa recognition applicable to mean values of stratigraphic populations, but not to individuals. This diagram was based on the relationship between two parameters: (1) Lsn – standardized length of the rostrum solidum expressed in mm; and (2) AV – shape of the guard in ventral aspect expressed as a percentage. The derivation of both these parameters involves complex calculations dependent on several measurements of the length and diameter of the guard (see Schulz 1979, pp. 16–21, fig. 4)

The complex formula for the derivation of the standardized length (Lsn), which incorporates the standardized diameter [Dpn = 13.5 mm; = mean value for all *Belemnella* specimens from both Krons Moor and a second locality, Hemmoor, studied by Schulz – see Schulz 1979, p. 17], has some basic consequences for the rest of his taxonomic considerations. Defining the Lsn, Schulz intended to average its values. It was chosen to reduce the correction of the observed length of the rostrum solidum [Ls] and achieve a standardized length [Lsn] for all individuals. However, such a definition has the effect that similar values of Lsn can be reached by morphologically different guards. Long and stout guards can reach values of Lsn similar to short and slender ones; short and stout specimens with a slow growth in length and a fast increase in guard thickness may reach similar Lsn values to specimens with a fast growth in length and a slow increase in guard thickness. Finally, when the diameters of specimens oscillate around the standardized diameter [Dpn = 13.5 mm], then the primary taxonomic parameter (Lsn) will depend, in nearly 100%, solely on the length of the guard.

As a result of the shortcomings mentioned above, the variability area on the graphic diagram (see Schulz 1979, fig. 53) ascribed to particular species can be occupied by morphologically different guards. This is a simple consequence of the species concept adopted by him. Additionally, Schulz (1979) put less weight on many of the commonly used features in the taxonomic description of belemnite guards, such as SD, AA or FA. Instead, he proposed some other features, e.g. angles connected with the shape of the bottom of ventral fissure (WS1, WS2, WSm; compare Schulz 1979). The precise determination and measurement of such features is very ambiguous and their significance, expressed as ontogenetic curves, is questionable (Schulz 1979, fig. 47, p. 88).

Additionally, in the taxonomic interpretations, Schulz assumed a linear relationship of Qp/Dp [cross-section quotient and rostrum diameter at the protoconch; = VDP/DVDP // DVDP of this paper] in studied populations of *Belemnella* (Schulz 1979, pp. 92–93, figs 51–52). The correlation for these populations (R = 0.65; 0.62; 0.48; 0.82), is satisfactory only in the last case. In the other cases, the correlation is very low or there is no correlation at all. Despite this, Schulz interpreted these relationships as linear. However, such an interpretation is at odds with the small correlation coefficient [R²] calculated on the basis of the data of Schulz (1979, figs 51–52), which are as follows: fig. 51A, R² = 0.39; fig. 51B, R² = 0.43; fig. 52A, R² = 0.69; fig. 52B, R² = 0.24. Such small values of R² show that it is hard to argue in favour of any linearity between the features studied.

It seems that the assumption made by Schulz of the linear dependence of Qp/Dp was premature. Such an interpretation requires the assumption that during ontogeny the cross section of the guard at the protoconch will change from oval or slightly compressed laterally in juveniles, to dorso-ventrally compressed in adults.

The author's observation of the cross sections perpendicular to the axis of the guard show that ratios of diameters [Qp/Dp] in different species are stable throughout ontogeny, thus contradicting the observations of Schulz (1979). In the author's opinion, the relationship of Qp (VDP/DVDP of this paper) for individual species should be constant, varying around the mean values. Thus the relationship of Qp/Dp, should not be linear or even close to linear, it should rather show stability of these features, independently of diameter Dp (= DVDP). The linear relationships recognized by Schulz (1979) were actually misinterpreted by him (Schulz 1979, figs 51A, B and 52 A, B). A lack of such relationships, therefore a stability of Qp (=VDP/DVDP), is confirmed for the whole populations of *Belemnella* from Krons Moor (Text-fig. 7).

What is important, however, is that Schulz (1979) was the first not to carry out an *a priori* classification. His taxonomic discriminations result directly from statistical analysis.

ARTIFICIAL NEURAL NETWORKS (ANN)

Since the beginning of the 1980s, ANN have been applied to a broad spectrum of scientific disciplines, where problems of objective classification need to be solved. ANN is able to project complicated, especially non-linear functions, which dominate in nature. In earth

sciences ANN have yet rarely been applied, but its potential is widely recognized (see Remin 2008).

ANN are software programs, able to “learn”, on the basis of previously collected data. They arose from researches on artificial intelligence and try to imitate the structure and function of natural neural systems. ANN possess the most important features of natural neural systems: (1) they learn based on examples; (2) are resistant to incompleteness of input data; and (3) are able to generalize the knowledge.

ANN can solve very complex problems, which in many cases cannot be solved by conventional computer applications. The collected data input sets are explored by specific algorithms that are able to learn.

The ANN are composed of “neurons”, basic units processing the data. The neurons are arranged in layers (Text-fig. 8): (1) the input layer (i.e. biometric features of belemnite guards); (2) the output layer (the results); and (3) hidden layers (those between the input and output layers). Based on the general structure of the neural network, two main groups of ANN are distinguishing: (1) multi-layer perceptrons, learned by backpropagation algorithm, and (2) the Kohonen self-organizing algorithm, also called self-organizing map [SOM]. Other ANN are less common. The type of ANN applied to solve a research topic depends on the nature of the topic and the problem to be resolved. More information on neuronal training, choosing the right algorithms and types of ANN can be found in, e.g., Kohonen (1982), Fausett (1994), Haykin (1994), Patterson (1996) and StatSoft (2006).

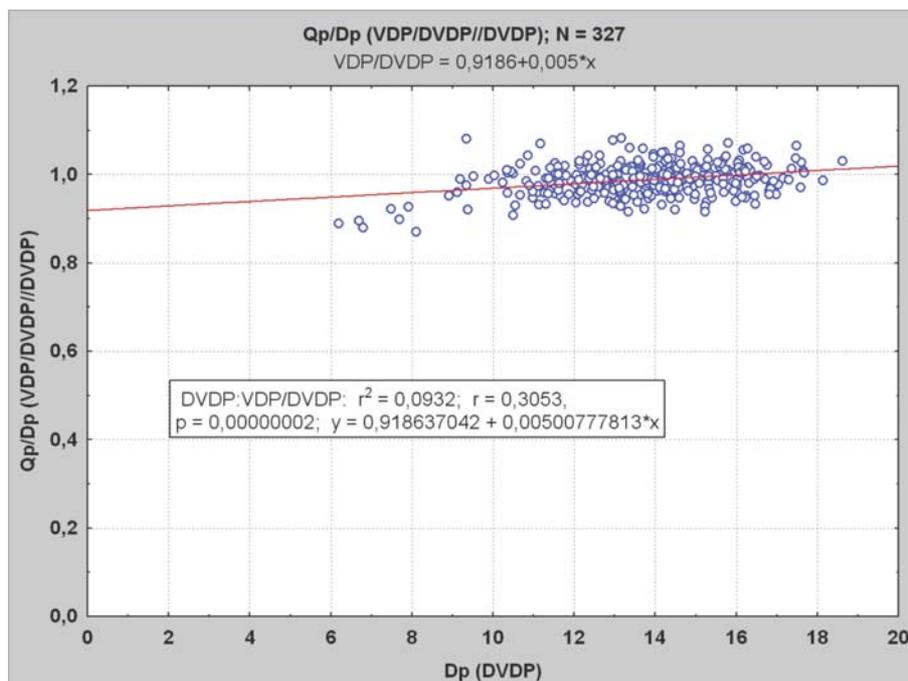
The Kohonen neural network [SOM]

Most of the ANN are designed to learn by a “supervised” procedure. It means that examples (input data) are presented simultaneously with known results (output data); the network is trained to learn the relationships between them.

For the analysis of the belemnite rostra performed herein, the Kohonen self-organizing mapping algorithm (SOM; compare Text-fig. 8) was used. The Kohonen SOMs are designed to learn “without the teacher” (Kohonen 1982; Fausett 1994; Haykin 1994; Patterson 1996; StatSoft 2006) and fall into the category of “unsupervised” networks; only input data (i.e. biometric features of the guards) are presented to the network.

As with other types of ANN the Kohonen networks use an iterative algorithm. The training process of the SOM is usually arranged in two steps: (1) a set of radial centres is chosen randomly; later (2) the algorithm modifies these centres to reflect the actual clusters coming from the input data.

The multidimensional hyperspace of the input data (in this case, a 29-multidimensional hyperspace, Text-fig. 8) is very difficult or sometimes impossible for a graphic presentation. Therefore it is converted into a two-dimensional topologic map (=self-organizing map, = SOM). This results in the loss of some information, but improves understanding and visualization of data (StatSoft, 2006).



Text-fig. 7. Scatter plot and regression line for $Qp/Dp [= (VDP/DVDP)//DVDP]$ for all specimens of *Belemnella* available from Kronsmoor

A well-trained Kohonen network creates a two-dimensional topologic map reflecting the mutual locations of studied objects based on the set of input data (e.g. features of belemnite guards) and can be interpreted as follows. The neurons or recognized groups of neurons located close to each other on the SOM will be activated by similar objects (guards); they will therefore represent clusters of similar input data (similar biometric data of belemnite guards), and hence will group similar rostra. On the other hand, different guards, defined by their biometric characteristics (Text-fig. 8), will activate neurons [or groups of neurons] located far from each other on the SOM.

The groups of neurons on the SOMs are concentrations of input data characterizing specific morphologic types of belemnite guards. Individual groups of neurons on the SOM represent the same morphologic type (= similar guards) and herein are provided with the same labels. The degree of similarity of the morphogroups distinguished is determined by their location on the SOM; groups located closer to each other are morphologically more similar than groups located farther from each other. Neurons described as “?” on the SOMs characterize an area of uncertainty. Their activation

does not allow an assignment of belemnite guards to recognized morphogroups.

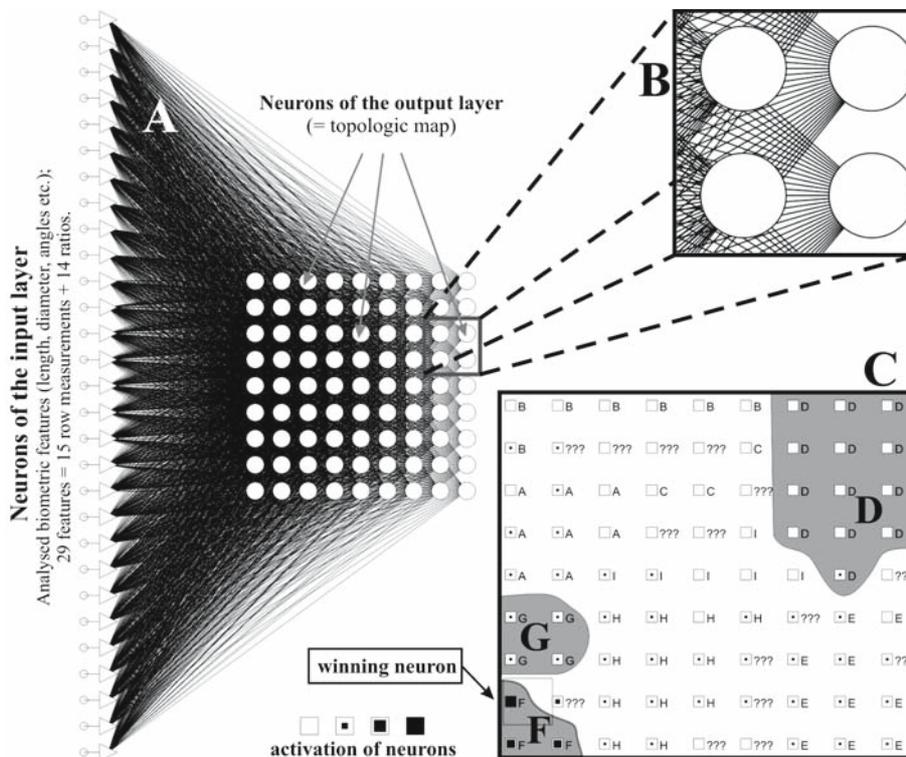
In all analyses, two-layer Kohonen neural networks with 29 inputs in the input layer (29 features that characterize each belemnite guard) have been used. The size of the SOM, which is the graphic answer of the network to the input data set, depends on the number of variables and cases studied, and is typically suggested by the algorithm used.

In order to simplify the interpretations and to improve the possibility of direct comparisons, the same morphogroup was labelled with identical letters in successive analyses. The morphogroups recognized by Kohonen network are further described using classic statistical methods.

SPECIES RECOGNITION BY THE KOHONEN NEURAL NETWORKS

Belemnella from Kronsmoor

In the first analysis, only complete guards were used (227 specimens), each characterized by 29 features



Text-fig. 8. **A**) structure of the applied self organized map (=SOM); 29 neurons in the input layer (the number of neurons reflects the number of biometric features used to characterize each guard); $9 \times 9 = 81$ neurons in the output layer = self organized map; **B**) the way in which the neurons are connected; each input neuron from the input layer is connected with 81 output neurons from the output layer; **C**) described SOM; individual letters characterize the concentration centres of similar input data (= similar values of features of belemnite guards, consequently similar guards; after Remin 2008)

(15 row data and 14 ratios). In the further analysis, both complete and incomplete guards were used (377). Subsequently, the morphogroups recognized by the Kohonen networks, regarded as representing natural populations, were analyzed using statistical methods.

In order to test the discrimination potential of the Kohonen neural networks, three analyses, differing in the degrees of stratigraphic homogenization, were performed:

Stratophenetic analysis (subdivision into four stratigraphic samples): The guards were subdivided into samples of possibly the smallest stratigraphic duration. The number of guards required for the analyses was the only limitation for the subdivision. Four samples, representing stratigraphic intervals of approximately 250–300 Ky, according to the estimation of Voigt and Schönfeld (2010), were distinguished.

Stratophenetic analysis (subdivision into two stratigraphic samples): The guards were subdivided into two samples.

One-step analysis: All guards, from the whole stratigraphic interval, were analyzed as a single sample.

Statistical verification of the recognized morphogroups

For all the morphogroups distinguished, plots of mean values of features and 95% confidence intervals were performed, in order to verify the hypothesis of equality or statistically significant differences between the means in distinguished morphogroups. For statistical analysis, only row data were used. Three types of relationships of compared means at 95% confidence intervals, may occur (Text-fig. 9A–C).

1. Means are markedly different and confidence intervals do not overlap (Text-fig. 9A); the means are significantly different.

2. Means are similar and confidence intervals overlap markedly (Text-fig. 9B); the means do not differ significantly.

3. Means are different but 95% confidence intervals overlap slightly (Text-fig. 9C); the means are most probably statistically different, although the verification needs other statistical tests.

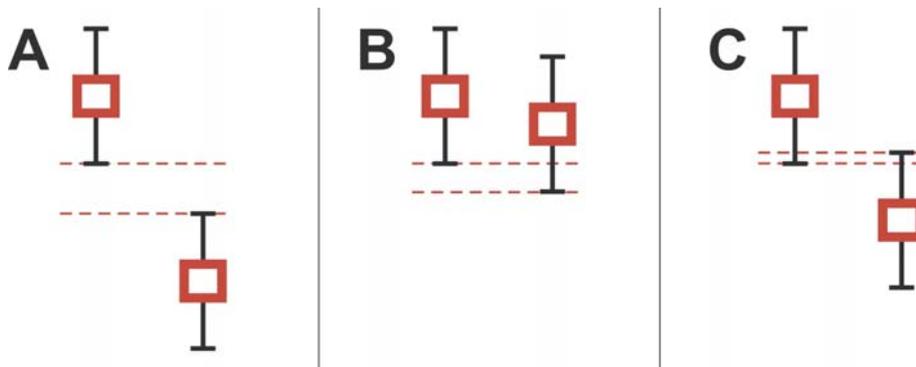
Since the recognized morphogroups can be easily discriminated using statistically different means of individual features (Text-fig. 9A), relationships like those illustrated in Text-fig. 12B, C have not been statistically verified, in order not to complicate the diagnosis of the recognized morphogroups (species).

Stratophenetic analyses of Belemnella from Kronsmoor (subdivision into four stratigraphic samples)

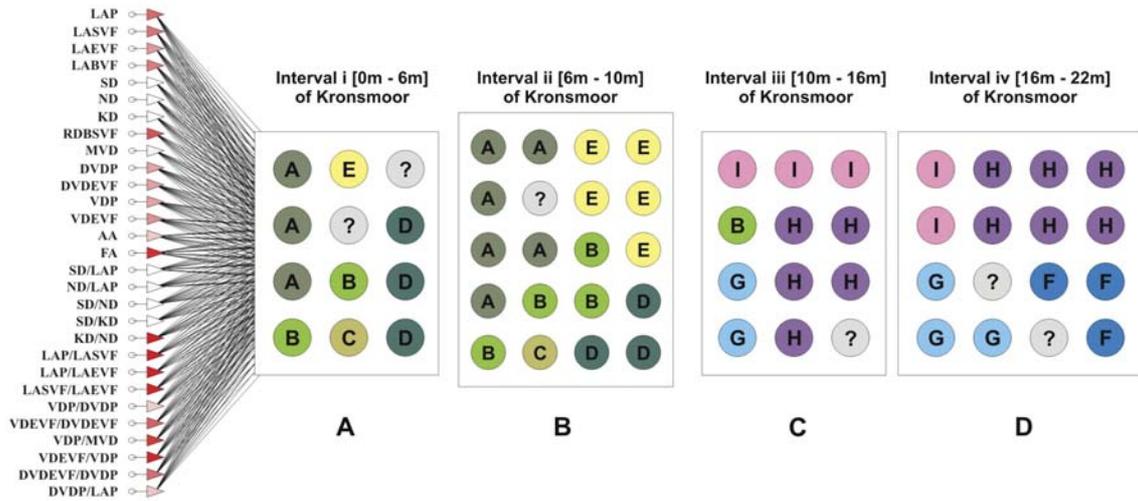
The material from the Kronsmoor section was subdivided into four stratigraphic samples: (i) F600 [= +0 m] to F600 + 6 m; (ii) F600 + 6 m to F600 + 10 m; (iii) F600 + 10 m to F600 + 16 m; and (iv) F600 + 16 m to F600 + c. 22 m.

Each sample was analyzed independently, using a two-layered Kohonen neural network (Text-fig. 10), with 29 inputs (29 parameters of the guard). The structures of the applied SOMs are shown in Text-fig. 10.

Exploration of the SOMs shows five distinct concentrations (morphogroups) in samples i and ii, labelled A through E (Text-fig. 10A, B), and four distinct concentrations (morphogroups) in samples iii and iv (Text-fig. 10C, D), labelled F through I. Such grouping was also confirmed by statistical analyses, which showed no significant differences between the groups labelled by the same letters (Text-figs 11, 12 and 13, 14). With the exception of group C from sample ii (Text-fig. 12), the means of the studied parameters of all the recognized morphogroups are characterized by small confidence intervals, implying a high morphological stability of the morphogroups. The relatively



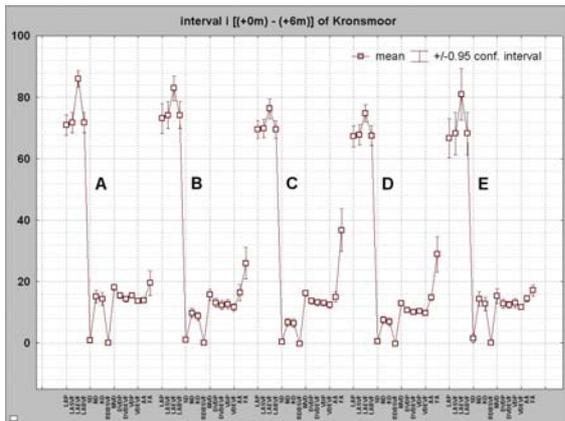
Text-fig. 9. Three main types of relationships of means recognized in the analyzed plots; for the interpretation, see text



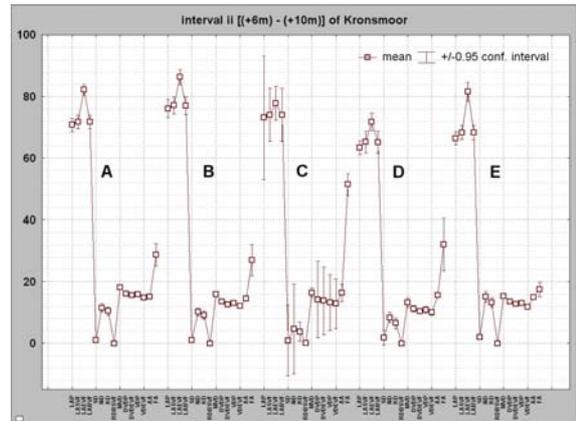
Text-fig. 10. A – 12 (3 × 4) neurons in the output layer with 48 guards analyzed from the interval i [(+0 m) – (+6 m)] of Kronsmoor; B – 20 (4 × 5) neurons in the output layer with 70 guards analyzed from the interval ii [(+6 m) – (+10 m)]; C – 12 (3 × 4) neurons in the output layer with 35 guards analyzed from the interval iii [(+10 m) – (+16 m)]; D – 16 (4 × 4) neurons in the output layer with 74 guards analyzed from the interval iv [(+16 m) – (+22 m)]

large confidence intervals observed in group C (Text-fig. 12) resulted from the small sample size of this group. However, comparing the mean values only,

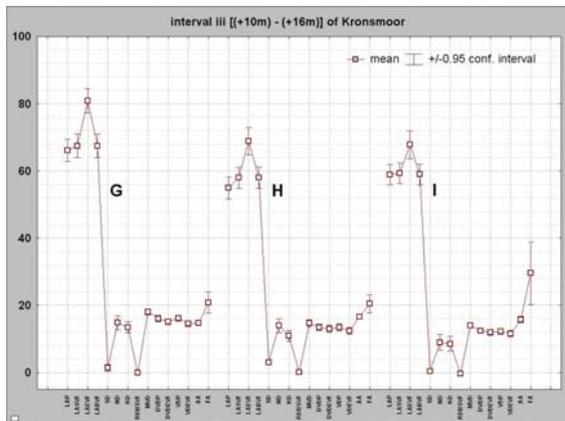
group C from both samples i and ii is homogeneous (Text-figs 11 and 12). Consequently, particular guard concentrations (morphogroups), labelled with the same



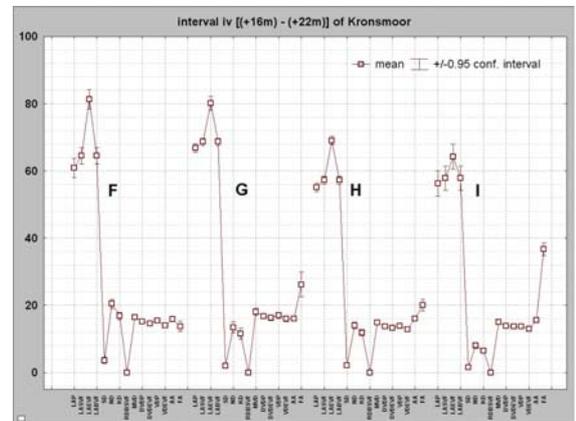
Text-fig. 11. Means and 95 % confidence intervals of features; groups A, B, C, D, E from the interval i [(+0 m) – (+6 m)] of Kronsmoor



Text-fig. 12. Means and 95 % confidence intervals of features; groups A, B, C, D, E from the interval ii [(+6 m) – (+10 m)] of Kronsmoor

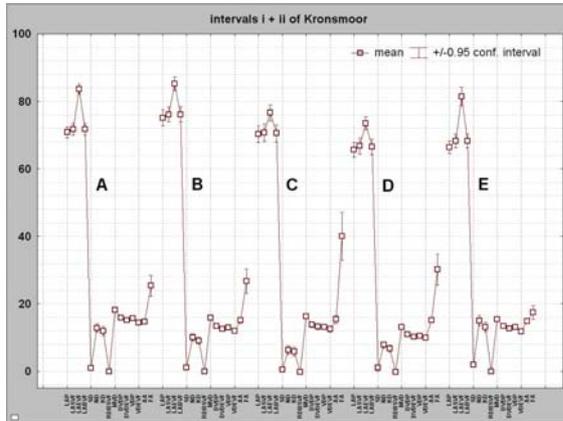


Text-fig. 13. Means and 95 % confidence intervals of features; groups G, H, I from the interval iii [(+10 m) – (+16 m)] of Kronsmoor

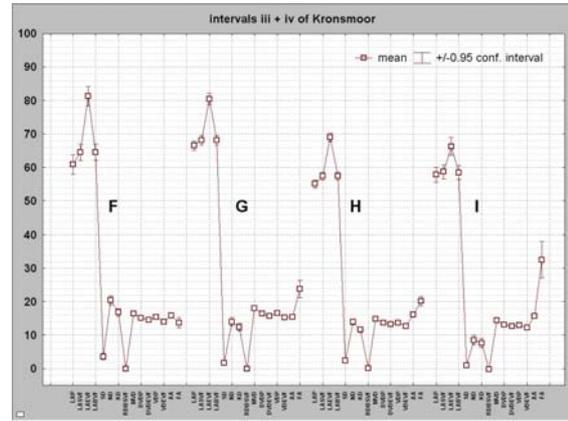


Text-fig. 14. Means and 95 % confidence intervals of features; groups F, G, H, I from the interval iv [(+16 m) – (+22 m)] of Kronsmoor

BELEMNELLA STRATIGRAPHY OF THE CAMPANIAN–MAASTRICHTIAN (CRETACEOUS) BOUNDARY



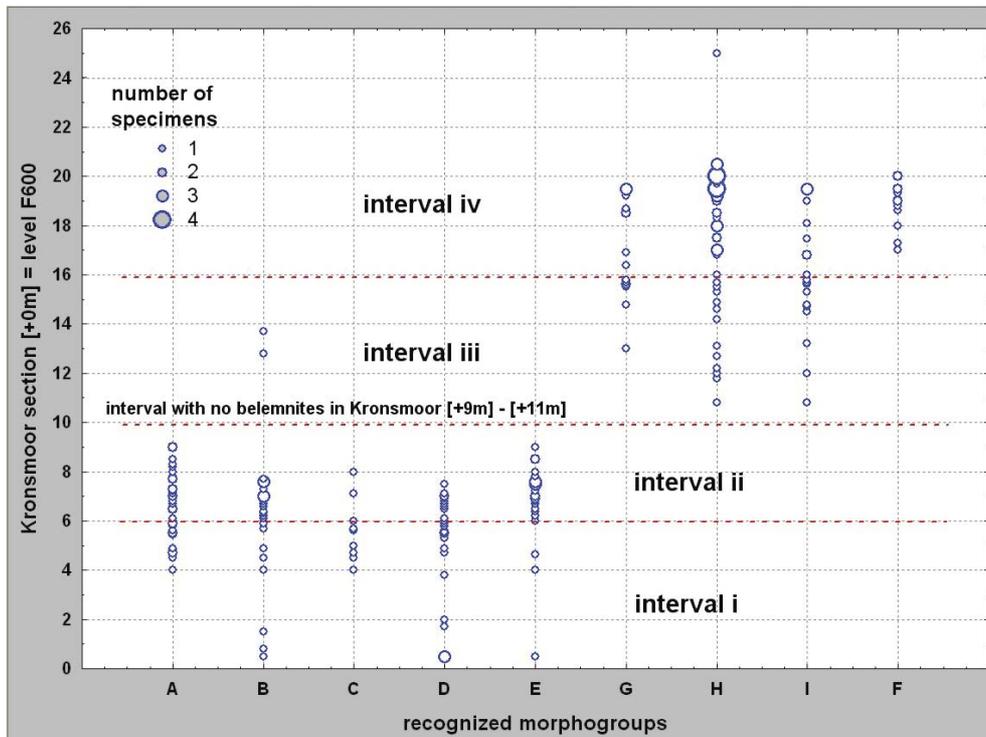
Text-fig. 15. Means and 95 % confidence intervals of features in groups A+A, B+B, C+C, D+D, E+E from two succeeding intervals i and ii [(+0 m) – (+6 m)] and [(+6 m) – (+10 m)].



Text-fig. 16. Means and 95 % confidence intervals of features in groups F, G+G, H+H, I+I from two succeeding intervals iii and iv [(+10 m) – (+16 m)] and [(+16 m) – (+22 m)].

letter in the analyses, are regarded as natural groups and classified accordingly. The relative position of particular morphogroups on the SOMs indicates the level of their similarity, and is interpreted further as natural similarity, i.e., corresponding to taxa. For example, in the hyperspace of sample i, group A is most similar to groups E and B, and least similar to groups C and D (such relationships are also confirmed by comparison of their mean values).

Summing up, five statistically significant morphogroups were recognized in samples i and ii, and four such groups in samples iii and iv (Text-fig. 17). Their stratigraphical distribution indicates that within the studied part of the Kronsmoor succession there are two intervals with more or less uniform belemnite faunas, the lower one, represented by samples i and ii, and the upper one, represented by samples iii and iv. Text-figs 15 and 16 show the statistical characteristics of groups



Text-fig. 17. Stratigraphic distribution of morphogroups recognized in Kronsmoor, based on stratophenetic analyses of four succeeding intervals i, ii, iii and iv

representing these two intervals; A, B, C, D, E, from the lower interval, and F, G, H, I, from the upper. Within these combined groups, the number of guards increased and hence the confidence intervals decreased, emphasizing the differences between the groups.

Stratophenetic analysis (subdivision into two stratigraphic samples)

In this analysis the guards were subdivided into two samples, I and II, corresponding to samples i+ii and iii+iv of the first analysis. Samples I and II are almost equal in size (118 and 109 specimens respectively), and represent c. 500 Ky each. Both samples were analyzed independently (Text-fig. 20A–B) using different architecture of the SOM.

Exploration of the SOMs allowed five and four distinct concentrations of neurons to be distinguished in samples I and II respectively (Text-figs 18A, B). The letters used in these analyses are the same as those used to denote particular morphogroups in the previous, four-step analyses.

Comparison of the results of the four-step and two-step analyses revealed very high similarities. The stratigraphic ranges and means of features of the distinguished morphogroups repeat those recognized in the stratophenetic analysis (compare Text-figs 19 and 15; 20 and 16). Small discrepancies observed between means were expected and can be explained by different number of guards and different structures of the SOMs in the analyses executed.

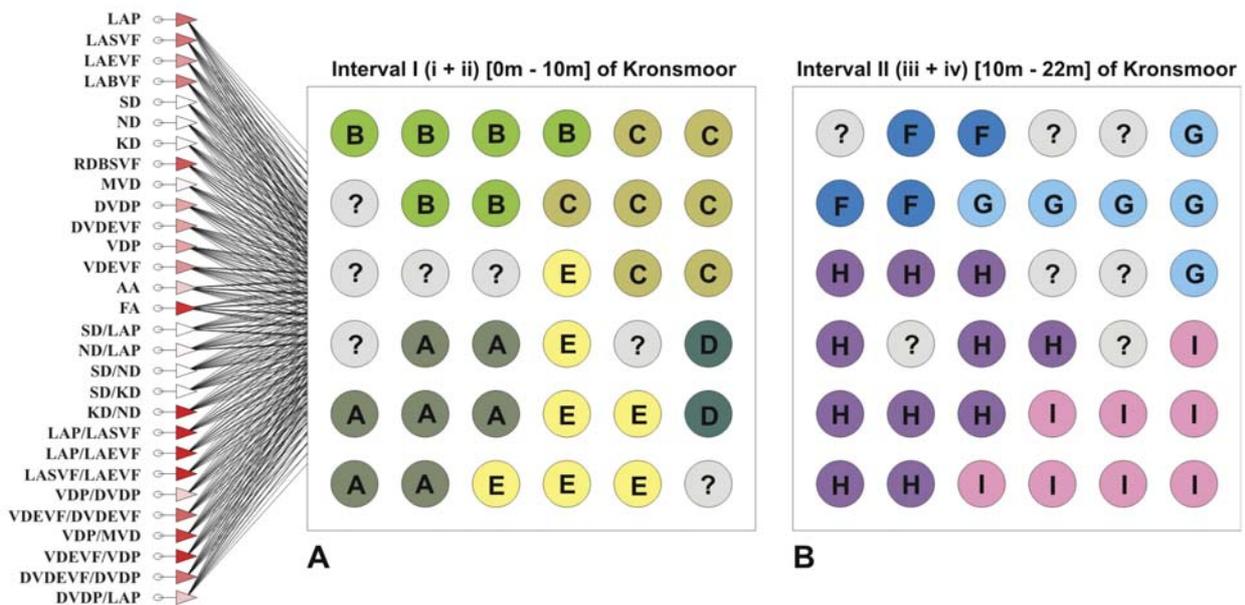
One-step analysis – without division

All complete belemnite guards (n = 227) with full biometry were treated in a single analysis. Exploration of the SOM allowed recognition of nine distinct morphogroups (Text-fig. 21).

Although the one-step analysis (Text-fig. 21) showed nine distinct concentrations, the same number as in the previous analyses, the morphospace of at least some of the groups is slightly different (Text-figs 22 and 23). The differences are clearly visible in groups A, D and E. In the stratophenetic analysis these groups are restricted to the interval +0m to +10m (Text-fig. 17), whereas in the one-step analysis, single specimens occur higher up in the section (Text-fig. 22). Similarly, groups G and H, which in the four-step analysis are limited to higher stratigraphic intervals (+10m to +22m), were also recognized in stratigraphically older samples (compare Text-figs 17 and 22).

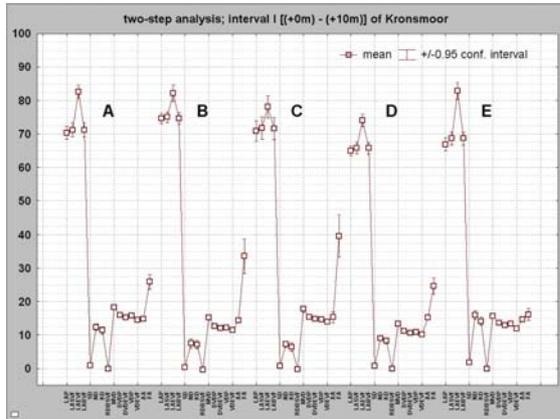
Discussion

Comparison of all the analyses shows that the application of Kohonen networks in taxonomic discrimination brings, as expected, the best results in the stratophenetic (four- or two-step) approach. A lack of major differences in the four- and two-step analyses, suggests a high morphological stability of the morphogroups within samples i-ii and iii-iv, with a main morphological turnover between them (stratigraphically, around the +10 m level of the Krons Moor section);

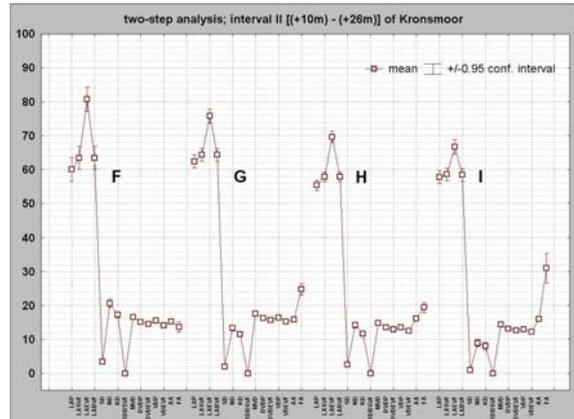


Text-fig. 18. **A** – 29 inputs, 36 (6 × 6) neurons in the output layer with 118 guards analyzed from interval I [(+0 m) – (+10 m)]; **B** – 29 inputs, 36 (6 × 6) neurons in the output layer with 109 guards analyzed from interval II [(+10 m) – (+22 m)]

BELEMNELLA STRATIGRAPHY OF THE CAMPANIAN–MAASTRICHTIAN (CRETACEOUS) BOUNDARY



Text-fig. 19. Means and 95 % confidence intervals of features; groups A, B, C, D, E recognized independently in the two-step analysis for interval I [(+0 m) – (+10 m)]; compare Text-fig. 20



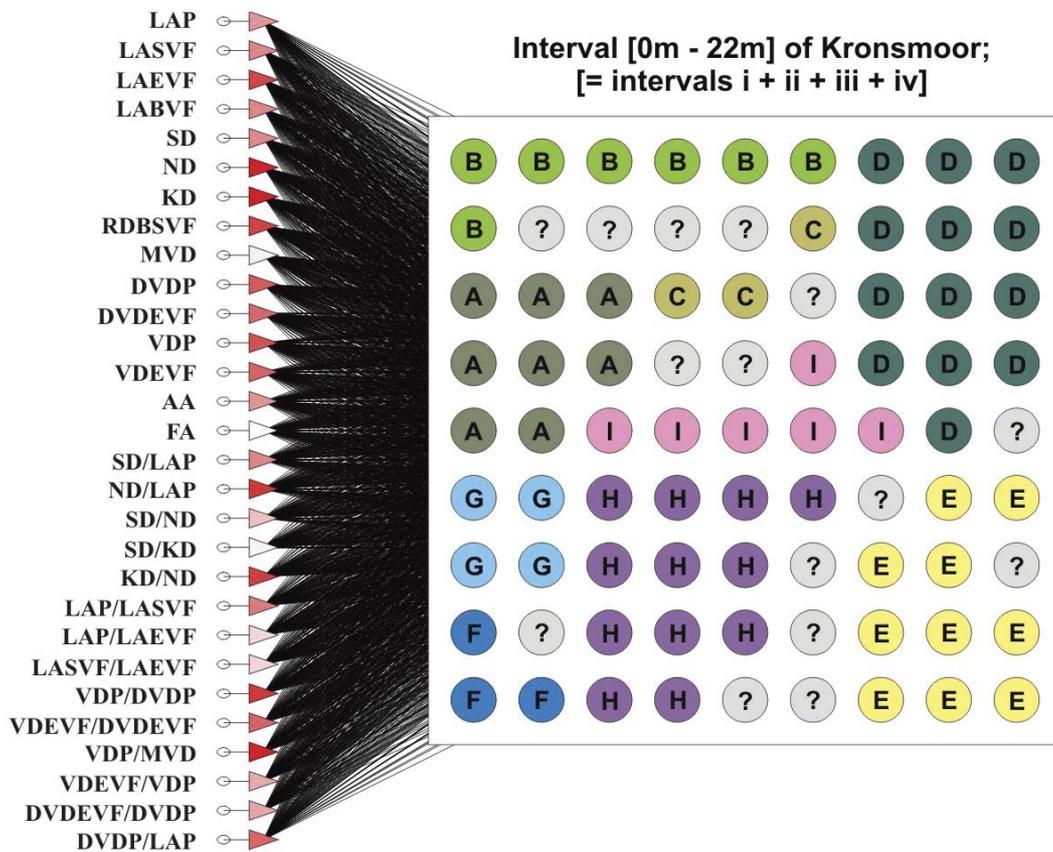
Text-fig. 20. Means and 95 % confidence intervals of features; groups F, G, H, I recognized independently in the two-step analysis for interval II [(+10 m) – (+22 m)]; compare Text-fig. 21

Text-figs 22, 23). In evolutionary terms, it suggests a punctualistic change within the early history of the genus *Belemnella*. Another possible explanation is a stratigraphic gap at the boundary between samples ii and iii, hiding intermediate steps of *Belemnella* evolution.

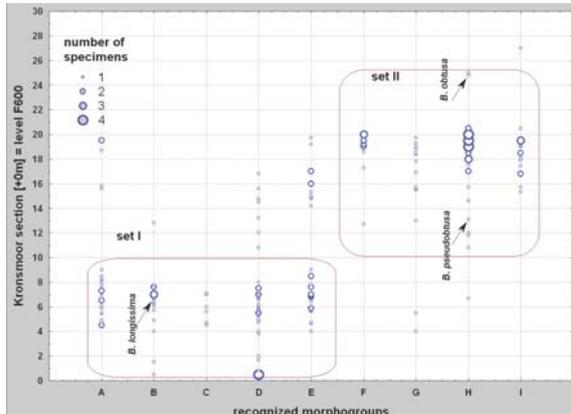
The one-step analysis, which seems to have definitely lower potential in taxonomic discrimination, re-

veals relationships between particular morphogroups that were not detected in any of the stratophenetic analyses. The most important ones are:

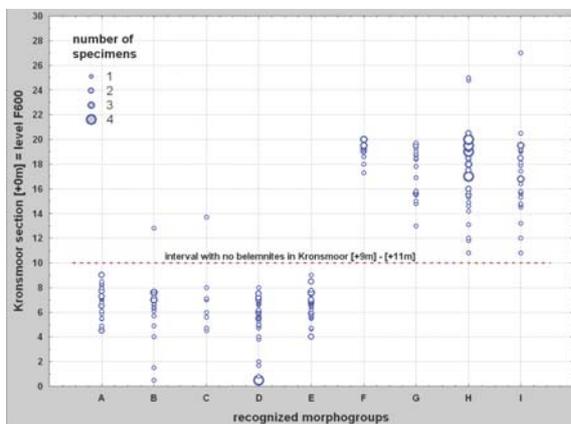
1. In group A, guards from the higher interval [(+15m) and higher] activate neurons of group G (set II; Text-fig. 22); it indicates morphological similarity between these groups.



Text-fig. 21. Structure of applied and described SOM used in the one-step analysis of all guards from the studied interval [(+0 m) – (+22 m)] of Kronsmoor



Text-fig. 22. Stratigraphic distribution of morphogroups recognized in the Krons Moor section based on the one-step analysis



Text-fig. 23. Stratigraphic distribution of morphogroups recognized in the Krons Moor section after final interpretation based on the one-step analysis

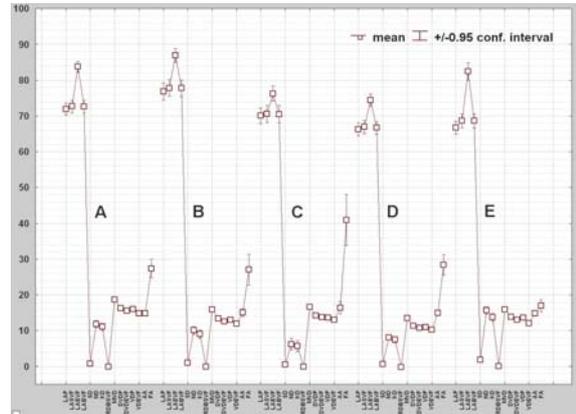
2. In group D, guards from the interval [(+10m) and higher] activate neurons of groups E and H (Text-fig. 22).
3. In group E, guards from the interval [(+10m) and higher] in most cases activate neurons of group H (Text-fig. 22).
4. In groups G and H, guards from interval [(+10m) and below] in most cases activate neurons of group E and A (set I; Text-fig. 22).

The power to reveal these relationships may potentially have a critical value in evolutionary interpretations of the whole clade.

Statistical verification of morphogroups from the Vistula and Krons Moor sections

Groups A, B, C, D, E

To verify the hypothesis that there were significant differences between morphogroups A–E, the means of particular features were analyzed according to the interpretations provided in Text-fig. 9.



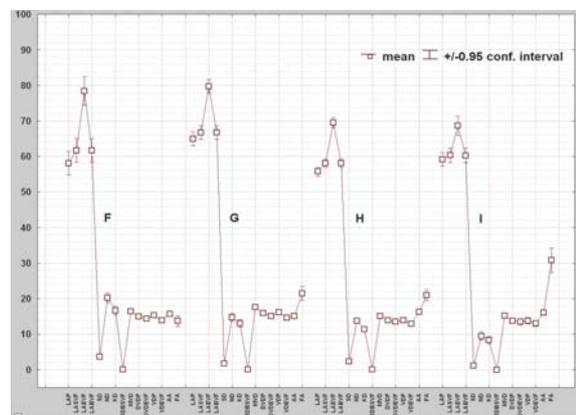
Text-fig. 24. Means and 95% confidence interval of features of complete specimens of the morphogroups A, B, C, D, E from the interval [(+0m) - (+10m)] of Krons Moor

In the Krons Moor section, groups A–E occupy the interval +0 m to +10 m; in the Vistula section it is the interval below the “boundary marl”. The plots (Text-fig. 24) show that means of particular features in morphogroups A–E differ markedly. The largest differences are between morphogroups located farthest from each other on the SOM (Text-figs 21 and 24). In most cases, statistically significant differences concern three or more characters between recognized morphogroups, allowing their easy separation.

Groups F, G, H, I

Similar analyses were carried out for morphogroups F, G, H and I, which occupy the interval +10 m and above, up to approximately the +22 m level in Krons Moor, and the interval above the “boundary marls” in the Vistula section.

Morphogroups F and G consists of longer and thicker forms in comparison with morphogroups H and I. Moreover, morphogroups F and G are characterized



Text-fig. 25. Means and 95 % confidence intervals of features in combined morphogroups F, G, H from the Vistula section and from the interval above +10 m of Krons Moor

by significantly higher values of the *internal-features* (Text-fig. 25) than observed in groups H and I. In respect of *internal-features*, group F is the most distinct, being characterized by guards with significantly different SD, ND and KD values compared with other morphogroups (Text-fig. 25). Additionally, group F can be easily recognized on the basis of its very low FA values. Such statistical differences between these groups are well in line with their position on the SOM, confirming the validity of the Kohonen networks classifications.

Belemnella from the Vistula section

Stratophenetic analysis cannot be applied to the Vistula material due to the insufficient size of most of the samples. Therefore, 50 complete and 34 incomplete guards were subjected to the one-step Kohonen network analysis, trained on the Krons Moor material. Every single specimen from the Vistula section was subjected to simulation using a trained Kohonen network (Text-fig. 21) and classified to one of the morphogroups (A through I) recognized in the Krons Moor section (Text-fig. 21). Five of these morphogroups (= taxa) can be assigned to known species; four are left in open nomenclature (see the Systematic Palaeontology part): These are as follows: A = *Belemnella* sp. A; B = *B. longissima*; C = *Belemnella* sp. C; D = *B. lanceolata*; E = *B. inflata*; F = *Belemnella* sp. F; G = *Belemnella* sp. G; H = *B. obtusa*; I = *B. vistulensis*.

Results

Raj section: Two *Belemnella* specimens are classified into group D [= *B. lanceolata*].

Raj N section: specimens are classified into groups B, D, and E [= *B. longissima*, *B. lanceolata*, *B. inflata* respectively]; a single specimens into group A [= *Belemnella* sp. A]. The Raj N belemnite assemblage is roughly equivalent to the Krons Moor assemblage from the interval +4m to +8m. As in Krons Moor, the guards of group D [= *B. lanceolata*] dominate.

Podole section: specimens from below the “boundary marl” are classified into group E [= *B. inflata*]; a few, not precisely located specimens, have activated neurons of groups H and I [= *B. obtusa* and *B. vistulensis*]. The belemnite assemblage from the Podole succession, below the “boundary marl”, is equivalent to the Krons Moor assemblage from the interval +6m to +10m.

Kłodzie N section: specimens from below the “boundary marl” are classified into groups D and B [= *B.*

lanceolata and *B. longissima*]. These taxa enable correlation of the Kłodzie N succession below the “boundary marl” with the interval +6m to +10m of the Krons Moor section, where guards of group D [= *B. lanceolata*] and B [= *B. longissima*], dominate around the +8m level.

Kłodzie S section: The specimens are from below and (a few) from above the “boundary marl”. They activated neurons mainly of morphogroup E [= *B. inflata*], and of morphogroups H and I [= *B. obtusa* and *B. vistulensis*], occurring in higher levels of both the Vistula and of Krons Moor sections (Text-figs 2, 3, 23). Hence, the belemnites of the Kłodzie S section correspond to the belemnites of the interval +8m to +12m of Krons Moor.

Przedmieście section: The specimens are referred to groups H, I and G [= *B. obtusa*, *B. vistulensis*, and *Belemnella* sp. G]. The last species is known exclusively from the Przedmieście section (Text-fig. 2). Therefore, this section can be roughly correlated with the interval +10m to +16m of Krons Moor, where representatives of morphogroup G appear for the first time and co-occur with *B. obtusa* and *B. vistulensis* (Text-figs 3, 23).

Dziurków section: The specimens activated neurons of morphogroups H, I and G [= *B. obtusa*, *B. vistulensis* and *Belemnella* sp. G]. Single specimens were included into morphogroup B [= *B. longissima*]. Incomplete guards were classified to morphogroups H and I, and also to group F [= *Belemnella* sp. F]. Because the presence of the last morphogroup is based on an incomplete specimen, its occurrence in Dziurków is indicated by a question mark (Text-figs 2). The Dziurków section may correlate with the interval +13m to at least +17 to +20m of Krons Moor.

SYSTEMATIC PALAEONTOLOGY

General Remarks

The understanding of the latest Campanian–early Maastrichtian European species of the genus *Belemnella* is still far from satisfactory. While the west European forms and biostratigraphic schemes are relatively well known (Schulz 1979), their relationships to forms known from eastern Europe (Jeletzky 1941; Naidin 1952; Nikitin 1958; Nadin and Beniamovskii 2006) remain poorly known. Even less is known about the so-called “primitive *Belemnella*” (i.e. *B. desnensis* and *B. licharewi*) as discussed by Jeletzky (1941,

1949a, 1951b, 1958). Consequently, evolutionary relationships and migratory patterns between western and eastern Europe remain highly speculative.

In 1979, Schulz recognized two subgenera within the early representatives of the genus *Belemnella* Nowak, 1913: (1) *Belemnella (Belemnella)* Nowak, 1913 and (2) *Belemnella (Pachybelemnella)* Schulz, 1979. As this subdivision was not revealed by the Kohonen neural network analysis applied herein, this subgeneric classification has not been followed.

Nine morphotypes revealed by the Kohonen neural network analysis are interpreted herein as distinct species. Five of them are referred to established species, while the remaining four are left in open nomenclature. Their final taxonomic interpretation requires further investigations, particularly comparison with East European material.

The species recognized in this investigation can be subdivided into two main groups, the *Belemnella longissima* group and the *Belemnella lanceolata* group. The *Belemnella longissima* group comprises *Belemnella longissima* Schulz, 1979, *Belemnella* sp. A, *Belemnella* sp. C, *Belemnella* sp. G and *Belemnella* sp. F. The *Belemnella lanceolata* group comprises *Belemnella lanceolata* (Schlotheim, 1813), *Belemnella inflata* (Arkhangelsky, 1912), *Belemnella vistulensis* (Kongiel, 1962) and *Belemnella obtusa* (Schulz, 1979). Both groups are characterized by a similar evolutionary pattern – being long, slender and lanceolate at the beginning of the clade and evolving to forms that are increasingly shorter and stout. Additionally, the younger forms are characterized by increasing values of the internal features and a decreasing fissure angle in comparison to older forms.

Size	small	medium	large or very large
LAP	< 60 mm	60 - 70 mm	> 70 mm
LAEVF	< 70 mm	70 - 80 mm	> 80 mm
MVD	< 15 mm	15 - 17 mm	> 17 mm
DVDP	< 13 mm	13 - 15 mm	> 15 mm
VDP	< 13 mm	13 - 15 mm	> 15 mm
Internal features			
SD	0 - 1 mm	1 - 2 mm	> 2 mm
ND	< 10 mm	10 - 15 mm	> 15 mm
KD	< 10 mm	10 - 15 mm	> 15 mm
AA	< 14°	14° - 16°	> 16°
FA	< 20°	20° - 30°	> 30°

Table 1. Ranges of size categories of selected external and internal features

The biometric characteristics presented herein are based on complete Krons Moor specimens. The size-ranges of selected parameters characterizing particular *Belemnella* species are summarized in Table 1. The descriptive terms and measurements used are shown in Text-figs 5, 6.

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; Kłodzie S – KłodzieS; Kłodzie N – KłodzieN; Przedmieście – Przedm.; Dziurków – Dziu.

Museum of the Geological and Paleontological Institute of the University of Hamburg [Geologisch-Paläontologisches Institut Hamburg]; specimens prefixed by Kx/xxx and S/xxx; e.g. KK810.

Family Belemnitellidae Pavlow, 1914

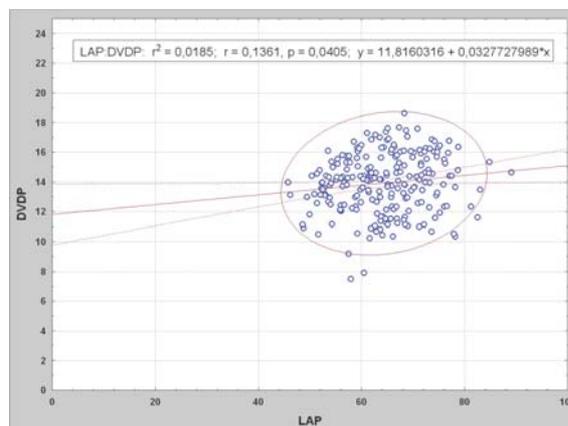
Genus *Belemnella* Nowak, 1913

[ICZN 1985, Opinion 1328; nr 2270]

TYPE SPECIES: *Belemnites lanceolatus* Schlotheim, 1813; p. 111; ICZN Opinion 1328 (1985), nr 2980.

DIAGNOSIS: Belemnitellidae with large guards. Length from apex to protoconch (LAP) up to 110 mm; alveolus cone-shaped and deep, with walls coated by “white layer”; guard markedly flattened ventrally. Alveolus connected with surface of guard through long ventral fissure. Alveolar angle (AA) between 10° and 21°; generally constant within genus. Ornamentation consisting of well-developed dorso-lateral longitudinal depressions, dorso-lateral double furrows undulating posteriorly, and of single lateral furrows. Vascular imprints well-developed but only in large forms commonly considered as adult; in small specimens, usually regarded as juveniles, weakly developed or absent. Schatsky distance (SD) short, generally less than 4 mm, commonly between 0 and 2.5 mm. Vascular imprints branching off dorso-lateral double furrows posteriorly, with angle larger than 30°. Relationship of LAP and DVDP strongly allometric (Text-fig. 26).

OCCURENCE: Widely distributed in the latest Campanian and Early Maastrichtian of the North European Biogeographic Province; also known from the northern peripheries of the Tethyan Realm and most probably from the North American Province.



Text-fig. 26. Scatter diagram, regression and 95 % confidence interval of the regression line; relationship of LAP and DVDP for all analysed specimens of the genus *Belemnella* from the Kronsmeer section

Belemnella longissima group

The *Belemnella longissima* group consists of five species, from oldest to youngest these are: *Belemnella longissima* Schulz, 1979, *Belemnella* sp. A, *Belemnella* sp. C, *Belemnella* sp. G and *Belemnella* sp. F. Within this group, a stable evolutionary pattern is observed. The oldest form – *B. longissima* is long or very long and slender whereas the younger forms, that is, *Belemnella* sp. A, *Belemnella* sp. G and *Belemnella* sp. F are characterized by progressively decreasing values of length features and fissure angle, with simultaneous increasing values of the internal characters.

Belemnella longissima Schulz, 1979

(Pl. 1; Figs 1–11)

pars 1979. *Belemnella longissima* n. sp.; Schulz, pp. 98–100, pl. 2, figs 3, 4, 6 [non pl. 2, fig. 1 = *Belemnella lanceolata*; non pl. 2, figs 2, 7–9 unclassified by ANN; non pl. 2 fig. 5 – not studied].

pars 1979. *Belemnella lanceolata* (Schlotheim, 1813); Schulz, pp. 95–97, pl. 1, figs 3, 6–8 [non pl. 1, figs 1, 4, 5 = *Belemnella lanceolata*; non pl. 1, figs 2, 9 = unclassified].

pars 1979. *Belemnella inflata* (Arkhangelsky, 1912); Schulz, pp. 107–110, pl. 6, fig. 9 [non pl. 6, figs 1, 8 = *Belemnella inflata*; non pl. 6, figs 2, 3, 6 = *Belemnella lanceolata*; non pl. 6, fig. 7 = *Belemnella* sp. C; non pl. 6, fig. 10 = *Belemnella vistulensis*].

HOLOTYPE: The holotype, KK408, SGPIH 2068, is the original of Schulz (1979; pl. 2, figs 3, 4; refigured herein Pl. 1, Figs 2a, 2b), from level mB/G606 + 0.6m

[= +7.1m above the level F600] of the Upper Campanian of Kronsmeer.

Biometric data of the KK408							
specimen	LAP	LASVF	LAEVF	LABVF	SD	ND	KD
KK408	82,57	85,37	89,07	84,77	2,80	6,49	3,69
RDBSVF	MVD	DVDP	DVDEVF	VDP	VDEVF	AA	FA
-0,60	15,23	11,59	11,10	11,81	11,26	13,00	45,50

PLESIOTYPE: KK214 from level mB606 – 0.3 m [= +5.7 m above the level F600] of the Upper Campanian of Kronsmeer. It was previously included in *B. inflata sensu* Schulz (1979).

Biometric data of the KK214							
specimen	LAP	LASVF	LAEVF	LABVF	SD	ND	KD
KK214	75,91	75,91	85,15	75,91	0,00	9,24	9,24
RDBSVF	MVD	DVDP	DVDEVF	VDP	VDEVF	AA	FA
0,00	16,95	13,80	12,90	13,37	12,28	13,89	26,56

MATERIAL: 21 complete specimens from Kronsmeer: KJ201, KJ703, KK014, KK214 (plesiotype), KK311, KK319, KK325, KK408 (holotype), KK419, KK422, KK514, KK519, KK524, KK607, KK609, KK616, KK625, KL608, S/BI46, KK512, KK626; 12 incomplete specimens from Kronsmeer: KJ401, KJ802, KJ907, KJ909, KK108, KK329, KK513, KK525, KK610, KK623, KL605, KL607; five complete specimens (RajN/016, RajN/032, RajN/060, KłudzN/005, Dziu/008) and one incomplete specimen (Podole/013) from the Vistula section.

DIAGNOSIS: Guard very long (mean LAP = 76.8 mm; max LAP up to 104 mm; mean LAEVF = 86.9 mm; max LAEVF = 114.2 mm); low values of all diameters; very slender in dorso-ventral and ventral view.

DESCRIPTION: Guards characterized by the longest guard of all Late Campanian [Tercis definition] species of the genus (LAP up to 104 mm; LAEVF up to 114.2 mm); slender and lanceolate in ventral view and slightly lanceolate or subcylindrical in lateral view; markedly compressed laterally at the ventral fissure, gaining characteristic lanceolate shape; slightly flattened ventrally. DVDP slightly larger than VDP; apical end moderately acute or acute with well-defined mucro.

SD small (mean 1.02 mm); ND and KD small to medium, with mean values 10.1 mm and 9.1 mm respectively; FA medium (mean 27.1°); AA medium (mean 15.1°). Shape of bottom of ventral fissure usually straight, sometimes slightly curved or undulating, with anterior deflection just before its junction with wall of alveolus.

Biometric characteristic and descriptive statistic of the group B (= <i>Belemnella longissima</i>)										
variables [mm] ^ - in degrees	N number of observations	Mean	Confidential interval: -95%	Confidential interval: +95%	Median	Minimum	Maximum	Variance	Standard Deviation	Standard Error
LAP	21	76,81	74,44	79,17	76,27	68,95	89,10	26,94	5,191	1,133
LASVF	21	77,82	75,47	80,18	77,13	70,88	89,10	26,71	5,168	1,128
LAEVF	21	86,91	84,99	88,83	85,97	81,39	98,38	17,81	4,220	0,921
LABVF	21	77,78	75,44	80,11	77,13	70,88	89,10	26,29	5,127	1,119
SD	21	1,02	0,60	1,44	1,13	0,00	2,80	0,86	0,927	0,202
ND	21	10,11	8,99	11,22	9,89	5,81	13,81	6,01	2,452	0,535
KD	21	9,09	7,93	10,25	9,44	3,69	12,24	6,49	2,547	0,556
RDBSVF	21	-0,05	-0,11	0,02	0,00	-0,60	0,00	0,02	0,150	0,033
MVD	21	15,89	15,21	16,57	15,79	12,32	18,30	2,23	1,495	0,326
DVDP	21	13,39	12,80	13,98	13,63	10,68	15,32	1,69	1,299	0,283
DVDEVF	21	12,52	11,89	13,16	12,63	9,61	14,78	1,94	1,392	0,304
VDP	21	12,98	12,42	13,54	13,37	10,17	15,01	1,51	1,230	0,268
VDEVF	21	11,96	11,41	12,51	12,28	9,11	14,33	1,45	1,204	0,263
AA*	21	15,06	14,00	16,13	14,51	11,94	21,99	5,48	2,342	0,511
FA*	21	27,06	22,71	31,41	24,21	13,14	45,50	91,34	9,557	2,086

Table 2. Biometry and descriptive statistics of *Belemnella longissima* [= morphogroup B]

Dorso-lateral longitudinal depressions and dorso-lateral double furrows, sometimes undulating posteriorly, well developed. Guard surface usually smooth, sometimes with weakly variably developed vascular markings.

REMARKS: The holotype and most of the topotype material of *B. longissima* Schulz, 1979 (9 of 15 specimens) were included into morphogroup B (= *B. longissima*). A few specimens classified by Schulz (1979) as *B. lanceolata*, *B. inflata*, and *B. desnensis* (compare the synonymy) fall also into morphogroup B [= *B. longissima*]. Therefore, I interpret morphogroup B as *Belemnella longissima* Schulz, 1979.

B. longissima differs from *Belemnella* sp. A in slightly larger values of *length-features* with simultaneously smaller values of diameters (Text-fig. 24). Thus, *B. longissima* is characterized by a longer and more slender guard.

From *Belemnella* sp. C, *B. longissima* differs in larger values of *length-features*; diameters are generally smaller than in *Belemnella* sp. C; for DVDEVF and VDEVF the differences are statistically significant (Text-fig. 24). The FA is markedly larger in *Belemnella* sp. C than in *B. longissima*.

The comparison of *B. longissima* and *B. lanceolata* shows that all *length-features*, all diameters and ND are significantly different and larger in *B. longissima* (Text-fig. 24).

With respect to *B. inflata*, *B. longissima* is characterized by significantly larger *length-features* (Text-fig. 24). The ND and KD are statistically significantly larger in *B. inflata*. In addition, *B. inflata* is characterized by a very small fissure angle, which is significantly smaller than in *B. longissima*.

OCCURRENCE: In the Vistula section, *B. longissima* is known from Raj N, Kłudzie N and Dziurków (Text-fig. 2) and it is moderately common. In Krons Moor, *B. longissima* appears at level F600 or slightly above. This taxon is most frequent in the interval +4 m to +8 m of Krons Moor, however single specimens were recognized higher up in the section (Text-fig. 3).

Belemnella sp. A

(Pl. 2; Figs 1–8)

pars 1979. *Belemnella* (*P.*) *inflata* (Arkhangelsky, 1912); Schulz, pp. 107–110, pl. 6, figs 4, 5 [only].

MATERIAL: 24 complete specimens from Krons Moor: KJ903, KK001, KK012, KK105, KK112, KK207, KK220 (type), KK310, KK415, KK425, KK428, KK502, KK506, KK517, KK533, KK615, KK702, KK704, KK705, KK802, KK901, KK507, KK628, KK904; seven incomplete specimens: KJ906, KK003, KK004, KK409, KK414, KK614, KK615; one complete specimen from the Vistula section: RajN/009; two incomplete specimens: RajN/056, RajN/067.

DESCRIPTION: Guard large to very large (mean LAP = 71.9 mm; max. LAP up to 78.8 mm; mean LAEVF = 83.8 mm; max LAEVF up to 91.7 mm), lanceolate or slightly lanceolate in ventral view and cylindrical, sub-cylindrical or slightly lanceolate in lateral view, late narrowing to apex. The guard is very stout, which generates extremely high values of maximal ventral diameter (mean MVD = 18.7 mm; max MVD up to 22 mm), almost not reported amongst other representatives of the genus *Belemnella* from the Upper Campanian and

Biometric characteristic and descriptive statistic of the group A (= <i>Belemnella</i> sp. A)										
variables [mm] ° - in degrees	N number of observations	Mean	Confidential interval: -95%	Confidential interval: +95%	Median	Minimum	Maximum	Variance	Standard Deviation	Standard Error
LAP	24	71,89	70,21	73,57	72,87	63,58	78,81	15,89	3,987	0,814
LASVF	24	72,68	70,89	74,47	73,49	63,58	81,39	17,98	4,241	0,866
LAEVF	24	83,76	82,26	85,25	84,05	77,51	91,71	12,53	3,540	0,723
LABVF	24	72,66	70,87	74,44	73,49	63,58	81,39	17,87	4,227	0,863
SD	24	0,79	0,37	1,21	0,00	0,00	2,87	1,00	1,002	0,205
ND	24	11,87	10,87	12,87	11,81	7,73	15,80	5,61	2,369	0,484
KD	24	11,08	10,08	12,07	10,34	7,73	14,73	5,61	2,368	0,483
RDBSVF	24	-0,02	-0,08	0,03	0,00	-0,59	0,00	0,01	0,120	0,025
MVD	24	18,66	18,26	19,07	18,88	16,60	19,94	0,93	0,965	0,197
DVDP	24	16,33	16,05	16,60	16,27	14,55	17,66	0,43	0,655	0,134
DVDEVF	24	15,60	15,33	15,86	15,70	14,28	16,76	0,39	0,623	0,127
VDP	24	16,08	15,78	16,38	16,06	14,41	17,82	0,52	0,719	0,147
VDEVF	24	14,84	14,60	15,09	14,91	13,84	15,75	0,33	0,575	0,117
AA*	24	14,88	14,43	15,33	14,98	12,61	16,79	1,13	1,063	0,217
FA*	24	27,38	24,83	29,92	26,50	18,80	38,00	36,36	6,030	1,231

Table 3. Biometry and descriptive statistics of *Belemnella* sp. A [= morphogroup A]

Lower Maastrichtian [Tercis definition]. The values of other diameters are also very high and significantly larger in comparison to any other species of the genus *Belemnella* considered in this paper. The guard is usually highly flattened ventrally over its entire length. DVDP is only slightly larger than (or almost equal to) VDP; apical end more or less obtuse, with a well defined mucro.

SD small (mean 0.79 mm); ND and KD medium-sized with means values of 11.9 mm and 11.1 mm respectively; FA medium (mean 27.4°); AA medium (mean 14.9°). Shape of the bottom of the ventral fissure is usually straight, sometimes slightly curved or undulating.

Dorso-lateral longitudinal depressions and dorso-lateral double furrows are well developed. The surface of the guard is usually smooth, sometimes with variably defined vascular markings.

REMARKS: The most typical specimen of *Belemnella* sp. A is KK 220, from level mB606 – 0.1 m [= +5.9 m above the level F600] of Krons Moor. This specimen is most similar to the means of the population of the morphogroup A and was previously classified by Schulz (1979) as *B. inflata*. It is from the Upper Campanian [Tercis definition].

Biometric data of the KK220								
specimen	LAP	LASVF	LAEVF	LABVF	SD	ND	KD	
KK 220	74,88	74,88	86,66	74,88	0,00	11,78	11,78	
	RDBSVF	MVD	DVDP	DVDEVF	VDP	VDEVF	AA	FA
	0,00	19,74	16,28	15,38	16,15	14,66	16,76	25,17

All specimens classified into morphogroup A were included by Schulz (1979) into *Belemnella (P.) inflata* (Arkhangelsky, 1912). However, *B. inflata sensu* Schulz has much broader morphological variability than *Belemnella* sp. A. The herein recognized *Belemnella* sp. A is

morphologically consistent and occurs in a narrow stratigraphic interval.

The very large values of diameters of *Belemnella* sp. A make it somewhat similar to *B. inflata*; however, according to the original diagnosis of the latter species (Arkhangelsky 1912, p. 609), its inflated and stout shape is connected with the apical region and not with the middle part of the guard, as in *Belemnella* sp. A. Therefore, representatives of *Belemnella* sp. A are left in open nomenclature.

Belemnella sp. A differs from *Belemnella* sp. C in its larger *length-features*; its diameters as well as ND and KD are significantly larger (Text-fig. 24). *Belemnella* sp. C is characterized by a significantly larger FA.

Belemnella sp. A differs from *B. lanceolata* in significantly larger values of all *length-features* as well as ND, KD and all diameters (Text-fig. 24).

From *B. inflata*, *Belemnella* sp. A differs in significantly larger diameters and FA; SD, ND and KD are markedly larger in *B. inflata* (Text-fig. 24). Additionally, in *inflata*, the MVD is usually at the posterior part of the guard, whereas in *Belemnella* sp. A it is located in the middle of the guard which gives it a more lenticular shape in ventral view.

OCCURRENCE: Rare in Raj N and Podole in the Vistula section; known from the interval +4.5m to +9m of Krons Moor; upper Campanian [Tercis definition].

Belemnella sp. G (Pl. 3; Figs 1–8)

pars 1979. *Belemnella (P.) obtusa* n. sp.; Schulz, pp. 114–118, pl. 9, figs 2, 6 [non pl. 9, figs 1, 3–4, 7 = *Belemnella obtusa*; non pl. 9, figs 5, 8 = *Belemnella vistulensis*].

Biometric characteristic and descriptive statistic of the group G (= <i>Belemnella</i> sp. G)										
variables [mm] * - in degrees	N number of observations	Mean	Confidential interval: -95%	Confidential interval: +95%	Median	Minimum	Maximum	Variance	Standard Deviation	Standard Error
LAP	19	64,99	62,99	66,99	64,88	57,78	71,87	17,23	4,151	0,952
LASVF	19	66,70	64,79	68,61	66,44	60,04	73,84	15,70	3,963	0,909
LAEVF	19	79,73	77,83	81,63	79,96	71,88	87,53	15,50	3,937	0,903
LABVF	19	66,70	64,79	68,61	66,44	60,04	73,84	15,70	3,963	0,909
SD	19	1,71	1,30	2,12	1,78	0,00	2,88	0,73	0,853	0,196
ND	19	14,74	13,62	15,87	15,13	10,12	18,00	5,47	2,338	0,536
KD	19	13,03	12,00	14,06	13,08	9,01	16,51	4,58	2,140	0,491
RDBSVF	19	0,00			0,00	0,00	0,00	0,00	0,000	0,000
MVD	19	17,59	17,10	18,07	17,46	15,94	19,79	1,01	1,007	0,231
DVDP	19	15,96	15,47	16,45	15,96	14,17	17,46	1,04	1,021	0,234
DVDEVF	19	15,10	14,57	15,62	14,83	13,28	16,96	1,20	1,094	0,251
VDP	19	16,11	15,68	16,55	16,05	14,79	18,09	0,82	0,903	0,207
VDEVF	19	14,65	14,21	15,09	14,56	12,78	16,36	0,83	0,909	0,209
AA*	19	15,12	14,65	15,60	15,22	13,24	16,69	0,98	0,989	0,227
FA*	19	21,47	19,49	23,46	21,54	15,51	30,89	17,01	4,124	0,946

Table 4. Biometry and descriptive statistics of *Belemnella* sp. G [= morphogroup G]

MATERIAL: 19 complete specimens from Kronsmeer: KL606, KM002, KM013, KM107, KM301, KM511 (type), KM516, KM623, KM702, KM707, KM811, KM923, KM008, KM106, KM706, KM805, KM813, KL910, KL903; six incomplete specimens: KM207, KM315, KM625, KM705, KN803, KM814; two complete specimens from the Vistula section: Dziu/006, Dziu/023; two incomplete specimens: Przed/008.

DESCRIPTION: Guards of medium size (mean LAP = 65.0 mm, up to 71.9 mm; mean LAEVF = 79.7 mm, up to 87.5 mm), with high values of *length-features*, largest among early Early Maastrichtian forms [Tercis definition] of Kronsmeer. Subcylindrical in ventral view and cylindrical, subcylindrical or slightly lanceolate in lateral view, with similar diameter over major part of guard. Guard stout and usually slightly flattened ventrally over entire length. DVDP slightly smaller than VDP. Apical end more or less obtuse, with well-defined mucro.

SD medium, with mean value 1.71 mm; ND and KD medium-sized with mean values 14.7 mm and 13.0 mm respectively; FA medium (mean 21.5°); AA medium (mean 15.1°). Bottom of ventral fissure usually straight. Dorso-lateral longitudinal depressions short and obscure; starting point of moderately developed dorso-lateral double furrows shifted anteriorly. Surface of guard almost smooth, sometimes with weakly defined vascular markings.

REMARKS: The most typical specimen is KM 511 from the level G620 – 6–7 m [= 18.5 m above the level F600] of the Lower Maastrichtian [Tercis definition] of Kronsmeer. This specimen is most similar to the means of the population of morphogroup G and was previously classified by Schulz (1979) as *B. obtusa*.

Biometric data of the KM511							
specimen	LAP	LASVF	LAEVF	LABVF	SD	ND	KD
KM 511	65,82	68,28	80,95	68,28	2,46	15,13	12,67
RDBSVF	MVD	DVDP	DVDEVF	VDP	VDEVF	AA	FA
0,00	16,60	15,96	15,64	16,06	15,17	15,81	21,76

All the specimens with complete biometry considered here as *Belemnella* sp. G were regarded by Schulz (1979) as representatives of *B. obtusa*.

Belemnella sp. G differs from *Belemnella* sp. F by markedly larger LAP and significantly smaller values of SD, KD and ND. All diameters are insignificantly larger in *Belemnella* sp. G. The described species is also characterized by markedly larger FA than in *Belemnella* sp. F (Text-fig. 25).

OCCURRENCE: Known from Przedmieście and Dziurków of the Vistula section; and from the interval between +13m and up to at least +20 m of Kronsmeer; Lower Maastrichtian [Tercis definition].

Belemnella sp. F (Pl. 4; Figs 1–9)

MATERIAL: 14 complete specimens from Kronsmeer: KM405, KM601, KM618, KM712, KM801, KM806, KM812, KM827, KM829 (type), KM903, KM909, KM921, KM606, KM830; one incomplete specimens from the Vistula section: Dziu/015.

DESCRIPTION: Guards small (mean LAP = 58.1 mm, up to 65.9 mm), LAEVF medium to large (mean LAEVF = 78.4 mm, up to 87.4 mm), slightly lanceolate in ventral view and cylindrical or subcylindrical in lateral view, with similar diameter over major part. Guards

Biometric characteristic and descriptive statistic of the group F (= <i>Belemnella</i> sp. F)										
variables [mm] * - in degrees	N number of observations	Mean	Confidential interval: -95%	Confidential interval: +95%	Median	Minimum	Maximum	Variance	Standard Deviation	Standard Error
LAP	14	58,11	54,80	61,43	58,43	45,82	65,86	32,94	5,740	1,534
LASVF	14	61,74	58,46	65,02	61,77	49,78	69,59	32,28	5,682	1,519
LAEVF	14	78,41	74,40	82,42	79,05	66,71	87,42	48,26	6,947	1,857
LABVF	14	61,74	58,46	65,02	61,77	49,78	69,59	32,28	5,682	1,519
SD	14	3,63	2,93	4,32	3,29	2,29	7,04	1,46	1,210	0,323
ND	14	20,30	18,90	21,70	20,58	15,41	23,92	5,91	2,432	0,650
KD	14	16,67	15,48	17,86	17,12	12,63	19,23	4,24	2,060	0,551
RDBSVF	14	0,00			0,00	0,00	0,00	0,00	0,000	0,000
MVD	14	16,41	15,83	16,99	16,79	14,56	17,88	1,00	1,002	0,268
DVDP	14	14,95	14,42	15,47	14,83	13,17	16,29	0,84	0,917	0,245
DVDEVF	14	14,31	13,62	15,00	13,80	12,64	16,44	1,42	1,193	0,319
VDP	14	15,34	14,69	15,99	15,25	13,69	17,23	1,26	1,123	0,300
VDEVF	14	13,85	13,20	14,51	13,54	12,26	15,77	1,28	1,132	0,303
AA*	14	15,68	15,10	16,26	15,51	14,03	17,52	1,01	1,004	0,268
FA*	14	13,70	12,21	15,18	13,29	9,92	18,56	6,61	2,570	0,687

Table 5. Biometry and descriptive statistics of *Belemnella* sp. F [= morphogroup F]

relatively stout and usually slightly flattened ventrally over its entire length. DVDP slightly smaller than VDP. Apical end markedly obtuse, with well-defined mucro.

Extremely large values of SD (mean = 3.63 mm); ND and KD very large with mean values 20.3 mm and 16.7 mm respectively; FA very small (mean 13.7°); AA medium (mean 15.7°). These values are maximal and minimal in the Early Maastrichtian [Tercis definition] *Belemnella* species (Text-fig. 25). Bottom of ventral fissure straight. Dorso-lateral longitudinal depressions and dorso-lateral double furrows moderately developed. Guard surface rather smooth, sometimes with variably defined vascular markings.

REMARKS: The most typical specimen is KM 829 from the level G615 + 2.5 m [= +19.5 m above the level F600] of the Lower Maastrichtian of Krons Moor. It is most similar to the mean values of the population of morphogroup F and was previously classified by Schulz as *B. obtusa*.

Biometric data of the KM829							
specimen	LAP	LASVF	LAEVF	LABVF	SD	ND	KD
KM 829	57,58	61,24	78,12	61,24	3,66	20,54	16,88
RDBSVF	MVD	DVDP	DVDEVF	VDP	VDEVF	AA	FA
0,00	17,25	15,74	15,42	15,92	14,51	15,48	14,04

All of the specimens with complete biometry considered here as *Belemnella* sp. F were regarded by Schulz (1979) as representatives of *B. obtusa*.

The concept of *B. obtusa sensu* Schulz, similarly to that of *B. inflata sensu* Schulz, is very broad. Thus, it was possible to distinguish morphologically coherent populations within his populations of *B. obtusa* and *B. inflata*. *Belemnella* sp. F is morphologically closest to *Belemnella* sp. G, as defined herein.

OCCURRENCE: Known from the Lower Maastrichtian [Tercis definition] of Dziurków, in the Vistula section, and from interval +17.3 m to +20 m of Krons Moor.

Belemnella sp. C (Pl. 5; Figs 1–7)

pars 1979. *Belemnella* (*P.*) *inflata* (Arkhangelsky, 1912); Schulz, pp. 107–110, pl. 6, fig. 7 [only].

MATERIAL: Eight complete [KJ910, KK008, KK215, KK222, KK521 (type), KK532, KK706, KL803] and four incomplete (KK204, KK221, KL802, KL702) specimens from Krons Moor.

DESCRIPTION: Guards medium to large (mean LAP = 70.1 mm; max up to 79.6 mm), LAEVF medium (mean LAEVF = 76.3 mm; max up to 87.1 mm), slightly lanceolate to lanceolate in ventral view, narrowing laterally in alveolar part and cylindrical or subcylindrical in lateral view; moderately flattened ventrally. DVDP slightly larger than VDP. Apical end obtuse or moderately acute or with well-defined mucro.

SD small (mean = 0.51 mm); ND and KD extremely small, with mean values of 6.2 mm and 5.7 mm; FA extremely large (mean = 41.0°). These values are minimal [SD, ND and KD] and maximal [FA] among all latest Campanian and Early Maastrichtian [Tercis definition] *Belemnella* species (Text-figs 24–25); AA medium (mean = 15.7°). Bottom of ventral fissure straight, sometimes curved or undulating.

Dorso-lateral longitudinal depressions weak; dorso-lateral double furrows moderately developed. Guard surface smooth with weakly defined vascular markings.

Biometric characteristic and descriptive statistic of the group C (= <i>Belemnella</i> sp. C)										
variables [mm] * - in degrees	N number of observations	Mean	Confidential interval: -95%	Confidential interval: +95%	Median	Minimum	Maximum	Variance	Standard Deviation	Standard Error
LAP	8	70,06	67,82	72,30	70,04	66,81	74,74	7,16	2,676	0,946
LASVF	8	70,57	68,18	72,96	71,18	66,81	74,74	8,18	2,860	1,011
LAEVF	8	76,29	74,22	78,36	76,82	73,03	80,17	6,15	2,480	0,877
LABVF	8	70,52	68,06	72,97	71,18	66,81	74,74	8,61	2,934	1,037
SD	8	0,51	0,01	1,01	0,36	0,00	1,52	0,36	0,596	0,211
ND	8	6,23	4,57	7,89	5,79	3,54	9,42	3,94	1,985	0,702
KD	8	5,72	4,18	7,26	5,45	3,54	8,67	3,39	1,840	0,651
RDBSVF	8	-0,05	-0,18	0,07	0,00	-0,44	0,00	0,02	0,155	0,055
MVD	8	16,63	16,09	17,18	16,53	15,47	17,58	0,43	0,654	0,231
DVDP	8	14,21	13,52	14,91	14,35	13,22	15,26	0,69	0,830	0,294
DVDEVF	8	13,75	13,03	14,46	13,75	12,66	15,07	0,73	0,852	0,301
VDP	8	13,64	13,03	14,24	13,85	12,53	14,44	0,52	0,718	0,254
VDEVF	8	13,05	12,56	13,55	13,17	12,27	13,97	0,35	0,593	0,210
AA*	8	16,43	14,66	18,19	16,53	13,18	20,00	4,46	2,112	0,747
FA*	8	40,97	33,77	48,17	40,07	31,38	51,68	74,18	8,613	3,045

Table 6. Biometry and descriptive statistics of *Belemnella* sp. C [= morphogroup C]

REMARKS: The most typical specimen is KK 521 from the level mB607 +/- 0.3 m [= +7 m above the level F600] of the Upper Campanian Krons Moor. It is most similar to the means of the population of morphogroup C; referred by Schulz (1979) to *B. inflata*.

Biometric data of the KK521								
specimen	LAP	LASVF	LAEVF	LABVF	SD	ND	KD	
KK 521	70,75	71,50	80,17	71,50	0,75	9,42	8,67	
	RDBSVF	MVD	DVDP	DVDEVF	VDP	VDEVF	AA	FA
0,00	16,33	14,34	14,06	14,44	13,23	14,42	31,38	

All of the specimens with complete biometry referred here to *Belemnella* sp. C were assigned to *Belemnella* (*P.*) *inflata* by Schulz (1979); some of the incomplete specimens were referred Schulz to *B. longissima* and *B. lanceolata*.

Belemnella sp. C differs from *B. lanceolata* in its larger values of ND and KD; all of the diameters as well as the FA are also significantly larger (Text-fig. 24).

From *B. inflata*, *Belemnella* sp. C differs in markedly smaller LAEVF as well as in distinctly smaller values of ND and KD. *B. inflata* differs also in its significantly larger SD and markedly smaller FA (Text-fig. 24).

OCCURRENCE: So far, known exclusively from the Upper Campanian of Krons Moor [Tercis definition], from the interval +4.5 m to +8 m.

Belemnella lanceolata group

The *Belemnella lanceolata* group consists of four species, from oldest to youngest these are: *Belemnella lanceolata* Schulz, 1979, *B. inflata* (Arkhangelsky, 1912) and, entering simultaneously, *B. obtusa* Schulz, 1979 and *B. vistulensis* (Kongiel, 1962). The evolu-

tionary pattern within this group is very similar to that observed in the *B. longissima* group. The older forms are long and slender whereas the younger forms, that is, *B. inflata*, *B. obtusa* and *B. vistulensis*, are shorter and stouter, with increasing values of the internal characters and decreasing values of the fissure angle.

Belemnella lanceolata (Schlotheim, 1813)

(Pl. 6; Figs 1–11)

1732. Breynius; Tab. Belemnitarum, figs 7–8 [after Birkelund, 1957].
1813. *Belemnites lanceolatus* (Schlotheim, 1813); p. 111 [after Schulz, 1979].
- pars 1975. *Belemnella lanceolata* (Schlotheim, 1813); Christensen, pp. 59–61, pl. 12, figs 1–4.
- pars 1979. *Belemnella lanceolata* (Schlotheim, 1813); Schulz, pp. 95–97, pl. 1, figs 1, 4–5; [non pl. 1, fig. 2, 9 = unclassified by ANN; non pl. 1, fig. 3, 6–8 = *Belemnella longissima*].
- pars 1979. *Belemnella longissima* n. sp.; Schulz, pp. 98–100, pl. 2, fig. 1 [only].
- pars 1979. *Belemnella inflata* (Arkhangelsky, 1912); Schulz, pp. 107–110, pl. 6, figs 2–3, 6 [non pl. 6 figs 1, 8 = *Belemnella inflata*; non pl. 6, figs 4–5 = *Belemnella* sp. A; non pl. 6, fig. 7 = *Belemnella* sp. C; non pl. 6, fig. 9 = *Belemnella longissima*; non pl. 6, fig. 10 = *Belemnella vistulensis*].
- pars 1979. *Belemnella desnensis* (Arkhangelsky, 1912); Schulz, pp. 110–112, pl. 7, figs 4, 6–8 [non pl. 7, fig. 1 = unclassified by ANN, holotype of *Belemnella* (*P.*) *desnensis* (Jeletzky, 1941); non pl. 7, figs 2–3 = unclassified by ANN, guards of *Belemnella licharewi* Jeletzky, 1949; non pl. 7, fig. 5 = not studied; non pl. 7, figs 9–10 = *Belemnella inflata*].

TYPE: Specimen illustrated by Breynius (1732, Tab. Belemnitarum, figs 7–8);

MATERIAL: 35 complete (KJ101, KJ202, KJ301, KJ701, KK007, KK013, KK021, KK102, KK103, KK110, KK205, KK210, KK213, KK218, KK225, KK307, KK324, KK332, KK412, KK416, KK430, KK433, KK511, KK515, KK516, KK523, KK605, KK624, KK708, S/BI23, S/BJ24, S/BK25, S/BK29, KK313, KK529) and 13 incomplete (KJ001, KJ702, KJ902, KK208, KK211, KK216, KK217, KK219, KK226, KK330, KK335, KK413, KK522) specimens from Krons Moor; 14 complete (Raj/081, Raj N/019, Raj N/022, Raj N/023, Raj N/027, Raj N/030, Raj N/037, Raj N/040, Raj N/046, Raj N/050, Raj N/071, Kłudz N/003, Kłudz N/008, Kłudz N/009, Kłudz N/001) and five incomplete (Raj/082, Raj N/048, Raj N/065, Raj N/066, Podole/005, Kłudz N/002) specimens from the Vistula section.

DIAGNOSIS: Guard medium-sized, lanceolate in ventral view, with relatively small values of ND and KD (mean ND = 8.1 mm; KD = 7.5 mm) and the smallest values of all diameters of all Late Campanian and Early Maastrichtian [Tercis definition] *Belemnella* forms; distinctly lanceolate in ventral view.

DESCRIPTION: Guards medium to large (mean LAP = 66.3 mm; max up to 86.2 mm), with medium LAEVF (mean LAEVF = 74.5 mm; max up to 90.4 mm), lanceolate or slightly lanceolate in ventral view, narrowing laterally in alveolar part and slightly lanceolate or sub-cylindrical in lateral view; slender and markedly flattened ventrally over its entire length; with DVDP slightly larger than VDP. Apical end usually acute, with rather poorly defined mucro.

SD small (mean = 0.64 mm); ND and KD small, with mean values 8.1 mm and 7.5 mm, respectively; FA relatively large (mean = 28.4°); AA medium (mean = 15.0°). Bottom of ventral fissure variable, usually straight, slightly curved or undulating, sometimes with posterior deflection just before junction with wall of alveolus.

Dorso-lateral longitudinal depressions well developed; dorso-lateral double furrows moderately developed; guard surface usually smooth, with rather weakly defined vascular markings.

REMARKS: The specimens with complete and incomplete biometry of morphogroup D, interpreted herein as *Belemnella lanceolata*, were referred by Schulz (1979) mostly to *B. inflata* and partly to *B. lanceolata*, *B. longissima*, *B. desnensis*, *B. obtusa* and *B. pseudobtusa*. It is noteworthy that most of the specimens classified by Schulz (1979) as *B. lanceolata* fall into morphogroup D in the present study.

Schulz (1979) stated that *B. lanceolata* is actually a very rare species in the Krons Moor section and he explained that he had recognized the eponymous zone only because the entry of this species was commonly regarded at that time as marking the base of the Maastrichtian. In Krons Moor the belemnite assemblage of this zone is actually dominated by his *B. inflata*.

Schulz (1979) also included into the synonymy of *B. lanceolata*, a sample of 42 specimens from Balsvik (Schonen, Sweden), analyzed biometrically by Christensen (1975). This latter study allows comparison of the population of *B. lanceolata* from Balsvik with the recognized morphogroup D [= *B. lanceolata*]. Some of the features (LASVF, LABVF, ND, KD, RDBSVF) were calculated from the biometric data reported by Christensen (1975).

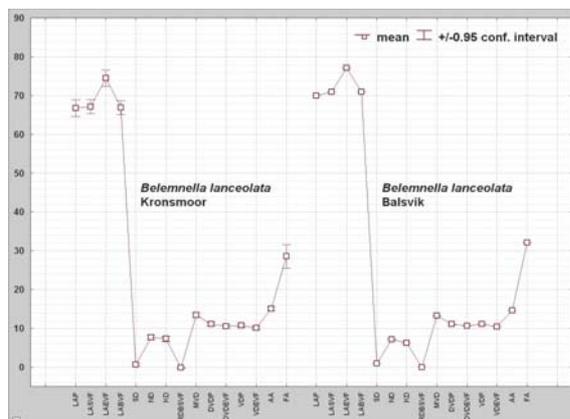
Biometric characteristic and descriptive statistic of the group D (= <i>Belemnella lanceolata</i>)										
variables [mm] * - in degrees	N number of observations	Mean	Confidential interval: -95%	Confidential interval: +95%	Median	Minimum	Maximum	Variance	Standard Deviation	Standard Error
LAP	35	66,31	64,48	68,14	65,91	57,52	78,22	28,36	5,325	0,900
LASVF	35	66,95	65,12	68,79	66,83	57,97	78,22	28,54	5,342	0,903
LAEVF	35	74,46	72,78	76,13	74,62	64,98	84,48	23,77	4,875	0,824
LABVF	35	66,72	64,97	68,47	66,48	57,97	77,29	25,91	5,090	0,860
SD	35	0,64	0,28	1,00	0,00	0,00	4,61	1,10	1,050	0,177
ND	35	8,14	7,37	8,92	8,04	3,52	14,14	5,09	2,255	0,381
KD	35	7,51	6,72	8,29	7,66	3,52	12,68	5,19	2,277	0,385
RDBSVF	35	-0,23	-0,39	-0,07	0,00	-2,13	0,00	0,22	0,473	0,080
MVD	35	13,56	12,92	14,19	13,34	8,40	16,92	3,42	1,848	0,312
DVDP	35	11,31	10,82	11,80	11,31	7,49	15,68	2,03	1,425	0,241
DVDEVF	35	10,71	10,24	11,18	10,87	7,31	15,09	1,88	1,371	0,232
VDP	35	11,02	10,51	11,53	11,03	6,91	15,33	2,18	1,478	0,250
VDEVF	35	10,31	9,85	10,78	10,36	6,66	14,62	1,85	1,362	0,230
AA*	35	15,00	14,54	15,46	14,95	12,51	18,82	1,80	1,343	0,227
FA*	35	28,38	25,50	31,27	27,76	12,74	48,97	70,54	8,399	1,420

Table 7. Biometry and descriptive statistics of *Belemnella lanceolata* [= morphogroup D]

The means and calculated 95% confidence intervals of the population of *B. lanceolata* from Balsvik are as follows: LAP = 70.01 \pm 2.4; LAEVF = 77.15 \pm 2.55; SD = 0.94 \pm 0.17; MVD = 13.25 \pm 0.66; DVDP = 11.14 \pm 0.52; DVDEFV = 10.69 \pm 0.50; VDP = 11.09 \pm 0.52; VDEFV = 10.48 \pm 0.50; AA = 14.64 \pm 0.37; FA = 32.12 \pm 4.3.

Based on the calculated means and 95% confidence intervals of the population of *B. lanceolata* from Balsvik, it can be concluded that this population is morphologically identical with morphogroup D from Kronsnoor and that none of the tested parameters differed significantly from each other (Text-fig. 27).

Taking into consideration the fact that belemnites from Balsvik have traditionally been referred to *B. lanceolata*, I interpret morphogroup D as representing *B. lanceolata* (Schlotheim, 1813).



Text-fig. 27. Comparison of two populations referred to *Belemnella lanceolata* [= morphogroup D] from Kronsnoor and from Balsvik, Schonen, Sweden

B. lanceolata differs from *B. inflata* in its markedly smaller values of LAEVF, ND and KD as well as of all of the diameters; FA is significantly larger in *B. lanceolata* (Text-fig. 24).

OCCURRENCE: Known from the topmost Campanian [Tercis definition] of Raj, Raj N, Podole and Kłudz S of the Vistula section, and from the interval +0 m to +9 m of the Upper Campanian [Tercis definition] of Kronsnoor. Also reported from Balsvik, Sweden, apparently from the same stratigraphic interval.

Belemnella inflata (Arkhangelsky, 1912)

(Pl. 7, Figs 1–8)

1912. *Belemnella lanceolata* var. *inflata* Arkhangelsky, 1912, p. 609.
pars 1979. *Belemnella* (*P.*) *inflata* (Arkhangelsky, 1912);

Schulz, pp. 107–110, pl. 6, figs 1, 8 [non pl. 6 figs 2–3, 6 = *Belemnella lanceolata*; non pl. 6, figs 4–5 = *Belemnella* sp. A; non pl. 6, fig. 7 = *Belemnella* sp. C; non pl. 6, fig. 9 = *Belemnella longissima*; non pl. 1, fig. 10 = *Belemnella* sp. I].

pars 1979. *Belemnella* (*P.*) *desnensis* (Jeletzky, 1941); Schulz, pp. 110–112, pl. 7, figs 9–10 [non pl. 7, fig. 1 = unclassified by ANN, holotype of *Belemnella* (*P.*) *desnensis* (Jeletzky, 1941); non pl. 7, figs 2–3 = unclassified by ANN, guards of *Belemnella licharewi* Jeletzky, 1949; non pl. 7, figs 4, 6–8 = *Belemnella lanceolata*; non pl. 7, fig. 5 = lost].

TYPE: Not yet determined – compare Schulz (1979) for discussion.

MATERIAL: 30 complete (KJ901, KK009, KK010, KK201, KK203, KK209, KK212, KK321, KK322, KK407, KK411, KK417, KK418, KK431, KK520, KK526, KK603, KK606, KK611, KK627, KK803, KK804, KK903, KJ704, KK229, KK432, KK309, KK423, KK601, KK602) and 20 incomplete (KJ801, KJ908, KK015, KK104, KK206, KK224, KK228, KK231, KK317, KK320, KK323, KK328, KK336, KK403, KK503, KK530, KK621, KK303, KK006, KK111) specimens from Kronsnoor: Also, 7 complete (Raj N/001, Raj N/002, Raj N/051, Raj N/033, Raj N/052, Podole/001, Podole/016) and 7 incomplete (Raj N/054, Raj N/063, Raj N/068, Podole/028, Kłudz S/004, Kłudz S/007, Raj N/042) specimens from the Vistula section.

DIAGNOSIS: Guard medium to large; relatively stout, inflated and lanceolate in ventral view. Large to very large values of ND and KD (mean ND = 15.7 mm; KD = 13.8 mm); extremely small values of FA (mean FA = 17°).

DESCRIPTION: Guard medium to large (mean LAP = 66.7 mm; max up to 86.8 mm) with large LAEVF (mean LAEVF = 82.4 mm; max up to 105.8 mm); lanceolate or slightly lanceolate in ventral view, narrowing laterally in alveolar part and slightly lanceolate in lateral view; slender and markedly flattened ventrally over its entire length; DVDP slightly larger than VDP. Apical end more or less obtuse, rarely moderately acute, with well-defined mucro.

SD medium (mean = 1.87 mm); ND very large and KD medium, with mean values of 15.7 mm and 13.8 mm, respectively; FA small (mean = 17.0°). AA medium (mean = 14.8°). Bottom of ventral fissure usually straight, sometimes slightly curved or undulating.

Dorso-lateral longitudinal depressions and dorso-lateral double furrows poorly developed; guard surface smooth, with weakly defined vascular markings.

Biometric characteristic and descriptive statistic of the group E (= <i>Belemnella inflata</i>)										
variables [mm] * - in degrees	N number of observations	Mean	Confidential interval: -95%	Confidential interval: +95%	Median	Minimum	Maximum	Variance	Standard Deviation	Standard Error
LAP	30	66,76	64,98	68,54	66,92	56,10	76,86	22,73	4,768	0,870
LASVF	30	68,62	66,64	70,61	68,43	56,10	79,06	28,33	5,323	0,972
LAEVF	30	82,43	80,01	84,86	82,53	69,54	96,75	42,06	6,486	1,184
LABVF	30	68,62	66,64	70,61	68,43	56,10	79,06	28,33	5,323	0,972
SD	30	1,87	1,37	2,36	1,80	0,00	5,99	1,73	1,317	0,240
ND	30	15,68	14,59	16,76	15,90	11,04	22,20	8,43	2,903	0,530
KD	30	13,81	12,68	14,94	13,36	8,93	19,75	9,12	3,020	0,551
RDBSVF	30	0,00			0,00	0,00	0,00	0,00	0,000	0,000
MVD	30	15,93	15,44	16,42	15,99	12,41	19,00	1,73	1,317	0,240
DVDP	30	13,88	13,46	14,29	13,82	10,45	15,93	1,24	1,114	0,203
DVDEVF	30	13,00	12,61	13,39	13,09	9,75	14,71	1,10	1,051	0,192
VDP	30	13,59	13,13	14,05	13,65	10,52	16,17	1,52	1,231	0,225
VDEVF	30	12,12	11,71	12,54	12,13	8,99	14,22	1,25	1,116	0,204
AA*	30	14,81	14,25	15,36	14,50	12,38	19,86	2,22	1,491	0,272
FA*	30	17,02	15,38	18,66	15,89	8,86	27,78	19,30	4,394	0,802

Table 9. Biometry and descriptive statistics of *Belemnella* sp. I [= morphogroup I]

DIAGNOSIS: Guards short, relatively stout, only slightly lanceolate or subcylindrical in ventral view and cylindrical in lateral view; low values of all *length-features* (mean LAP = 59.0 mm; mean LAEVF = 68.6 mm); SD medium (mean SD = 1.2 mm); ND and KD small; FA large (mean FA = 31°).

DESCRIPTION: Guards rather small (mean LAP = 59.1 mm, up to 68.3 mm; mean LAEVF = 68.6 mm, up to 81.8 mm), one of the smallest of all early Mastrichtian [Tercis definition] *Belemnella* species; slightly lanceolate to subcylindrical in ventral view and cylindrical in lateral view; relatively stout with similar diameter over major part of its length, especially in lateral view; slightly flattened ventrally over its entire length. DVDP only slightly larger than (or almost equal to) VDP. Apical end acute or slightly obtuse, with variably defined mucro.

SD medium to small (mean = 1.19 mm); ND and KD small, with mean values of 9.5 mm and 8.3 mm, respectively; FA medium to large (mean = 31°); AA medium to large (mean = 16.0°). Bottom of ventral fissure usually straight, sometimes slightly curved or undulating.

Dorso-lateral longitudinal depressions short and weak; starting point of moderately expressed dorso-lateral double furrows markedly shifted anteriorly. Guard surface usually smooth, with poorly defined vascular markings.

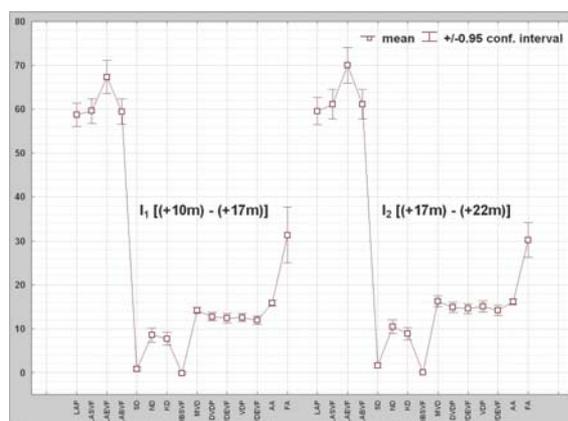
REMARKS: In 1962, Kongiel erected a new subspecies – *Belemnella gracilis vistulensis*, on the basis of specimens from Kłodzie and Przedmieście (Text-fig. 1) and a few specimens from Lwów (Ukraine). Since he never accepted the legitimacy of the genus *Belemnella* Nowak, 1913, the new subspecies was referred by

him to the genus *Belemnella* d'Orbigny, 1840. The present investigation using Kohonen network simulation trained on Krons Moor material, reveal that both the holotype and paratype of *vistulensis* fall into morphogroup I; however, both the holotype and paratype are a little bit smaller than the rest of the population (Pl. 8, Figs 11–12). Additionally, the description and ranges of critical characters provided by Kongiel (1962, pp. 56–57) also fit best with the morphogroup I. Therefore, the whole morphogroup I is interpreted here as representing Kongiel's species *Belemnella vistulensis*.

The most typical specimen that fits best the mean values of the population of *B. vistulensis* [= morphogroup I] is KM 312 from the level G615 – 0.25 m [= 16.8 m above the level F600] from the Lower Mastrichtian [Tercis definition] of Krons Moor (Pl. 8, figs 1a, b). Schulz (1979) referred it to his *B. obtusa*. The specimens with complete biometry, referred herein to *B. vistulensis*, were referred by Schulz (1979) to his *B. obtusa*, *B. pseudobtusa*, and *B. inflata*.

Biometric data of the KM312							
specimen	LAP	LASVF	LAEVF	LABVF	SD	ND	KD
KM 312	56,72	58,83	66,22	58,83	2,11	9,51	7,40
RDBSVF	MVD	DVDP	DVDEVF	VDP	VDEVF	AA	FA
0,00	13,51	12,44	12,30	12,01	11,39	15,31	29,75

Comparison of the means of particular features of younger and older representatives of *B. vistulensis* within its stratigraphic range shows that two forms can be distinguished: the older form (compare Text-fig. 28) is characterized by smaller values of all diameters than its younger form (Text-fig. 28), thus being slightly more slender at the same length than its younger representatives (Text-fig. 28).



Text-fig. 28. Means and 95 % confidence intervals of features in the sub-group I₁ and I₂ from different stratigraphic intervals of Krons Moor

B. vistulensis differs from *B. obtusa* in significantly smaller values of SD, KD and ND and in a markedly larger FA (Text-fig. 25).

From *Belemnella* sp. G it differs in significantly smaller values of all length-parameters, as well as all diameters, SD, ND and KD and in a markedly larger FA (Text-fig. 25).

B. vistulensis differs from *Belemnella* sp. F in significantly smaller values of LAEVF and diameters. The values of internal characters, SD, ND and KD, are twice as small in *B. vistulensis*. In addition, in comparison to *B. vistulensis* (FA = 31°), *Belemnella* sp. F is characterized by a very small FA c.a. 13.7° (Text-fig. 25).

OCCURRENCE: In the Vistula section, the species is known from the upper part of the Podole and Kłudzie S sections (around or above the “boundary marl”) and from the Przedmieścia and Dziurków sections. It also occurs in the interval between +11 m and +20 m (with a single specimen from the level +27 m) of Krons Moor. Additionally it is known from the vicinity of Lwów (Ukraine). Known exclusively from the Lower Maastrichtian [Tercis definition].

Belemnella obtusa Schulz, 1979

(Pl. 9, Figs 1–9)

pars 1979. *Belemnella* (*P.*) *pseudobtusa* n. sp.; Schulz, pp. 112–114, pl. 8, figs 4–8, 10 (figs 4–5 = holotype of *Belemnella* (*P.*) *pseudobtusa* n. sp. Schulz, 1979); [non pl. 8, figs 1 = lost, 3 = not studied, 9 = unclassified by ANN; non pl. 8, fig. 2 = *Belemnella* sp. I].

pars 1979. *Belemnella* (*P.*) *obtusa* n. sp.; Schulz, pp. 114–118, pl. 9, figs 1, 3–4, 7 (figs 4–5 = holotype of *Belemnella* (*P.*) *obtusa* n. sp. Schulz, 1979);

[non pl. 9, figs 2, 6 = *Belemnella* sp. G; non pl. 9, figs 5, 8 unavailable].

1999. *Belemnella* (*P.*) *obtusa*, Schulz, 1979; Christensen, pp. 120–122, pl. 4, figs 26–32.

HOLOTYPE: It is KN810, SGPIH 2123, the original of Schulz (1979, Fig. 62d, pl. 9, fig. 3, 4; pl. 12, fig. 9; re-figured here Pl. 9 Figs 1a, 1b), from the level G 620 [= +24.4 m above the level F600], of the Lower Maastrichtian of Krons Moor, Germany.

Biometric data of the KN810							
specimen	LAP	LASVF	LAEVF	LABVF	SD	ND	KD
KN 810	57,32	58,75	76,13	58,75	1,43	18,80	17,38
RDBSVF	MVD	DVDP	DVDEVF	VDP	VDEVF	AA	FA
0,00	14,36	14,25	13,93	13,80	13,50	15,25	12,44

PLESIOTYPE: The plesiotype, designated herein, is KM823, from the level G615 + 1–4 m [= +18 – +21m above the level F600], of the Lower Maastrichtian of Krons Moor. It fits best the mean values of the population of *Belemnella obtusa* as interpreted herein (compare Table 10). Schulz (1979) referred it to *B. obtusa*.

Biometric data of the KM823							
specimen	LAP	LASVF	LAEVF	LABVF	SD	ND	KD
KM 823	55,22	57,69	70,21	57,69	2,46	14,99	12,53
RDBSVF	MVD	DVDP	DVDEVF	VDP	VDEVF	AA	FA
0,00	15,51	14,32	14,17	14,82	13,67	15,58	20,86

MATERIAL: 45 complete specimens [KL104, KL301, KL405, KL603 (holotype of *B. pseudobtusa* Schulz, 1979), KM004, KM108, KM303, KM403, KM502, KM508, KM510, KM605, KM609, KM610, KM621, KM624, KM704, KM711, KM714, KM802, KM804, KM809, KM815, KM822, KM823 (plesiotype), KM833, KM916, KM917, KM918, KM920, KM922, KN802, KN810 (holotype of *B. obtusa* Schulz, 1979), KM006, KM009, KM406, KL905, KL908, KM001, KM103, KM205, KM304, KM305, KM834, KM919] and 16 incomplete specimens (KL002, KL403, KL408, KL501, KL604, KL805, KM010, KM012, KM104, KM105, KM109, KM506, KM619, KM832, KM915, KN504) from Krons Moor: Also, 14 complete specimens (Przed/004, Przed/009, Przed/011, Dziu/004, Dziu/009, Dziu/010, Dziu/020, Podole/009, Podole/015, Podole/025, Podole/030, Kłud S/001, Podole/003, Dziu/001) from the Vistula section.

DIAGNOSIS: Guards short, relatively stout, cylindrical or subcylindrical in ventral view, with low values of all length-features (mean LAP = 55.8 mm; mean LAEVF

Biometric characteristic and descriptive statistic of the group H (= <i>Belemnella obtusa</i>)										
variables [mm] * - in degrees	N number of observations	Mean	Confidential interval: -95%	Confidential interval: +95%	Median	Minimum	Maximum	Variance	Standard Deviation	Standard Error
LAP	45	55,77	54,49	57,06	55,36	46,25	67,11	18,27	4,275	0,637
LASVF	45	58,08	56,85	59,31	57,47	49,45	69,49	16,72	4,089	0,610
LAEVF	45	69,49	68,06	70,91	70,05	57,83	83,35	22,54	4,747	0,708
LABVF	45	58,08	56,85	59,31	57,47	49,45	69,49	16,72	4,089	0,610
SD	45	2,31	2,08	2,53	2,44	0,00	3,60	0,56	0,748	0,111
ND	45	13,71	13,04	14,39	13,32	8,59	19,05	5,00	2,237	0,333
KD	45	11,41	10,72	12,10	11,08	5,64	17,38	5,28	2,298	0,343
RDBSVF	45	0,00			0,00	0,00	0,00	0,00	0,000	0,000
MVD	45	15,06	14,68	15,44	15,23	12,08	18,21	1,56	1,249	0,186
DVDP	45	13,90	13,54	14,25	14,09	10,89	16,70	1,38	1,174	0,175
DVDEVF	45	13,47	13,09	13,85	13,36	10,22	16,45	1,60	1,267	0,189
VDP	45	13,91	13,52	14,30	13,80	10,62	17,17	1,69	1,300	0,194
VDEVF	45	12,90	12,51	13,29	12,88	9,24	15,91	1,69	1,299	0,194
AA*	45	16,24	15,98	16,51	16,15	14,78	18,50	0,76	0,874	0,130
FA*	45	20,93	19,38	22,48	20,86	10,24	38,13	26,58	5,155	0,769

Table 10. Biometry and descriptive statistics of *Belemnella obtusa* [= morphogroup H]

= 69.5 mm); SD relatively large (mean SD = 2.3 mm); FA medium (mean FA = 21°).

DESCRIPTION: Guard small, one of the smallest of all Early Maastrichtian [Tercis definition] *Belemnella* species (mean LAP = 55.8 mm; mean LAEVF = 69.5 mm); stout, slightly lanceolate in ventral view and cylindrical or subcylindrical in lateral view, with similar diameter over major part of its length; usually slightly flattened ventrally over its entire length. DVDP equal to VDP. Apical end markedly obtuse, with very well defined mucro.

SD large (mean = 2.30 mm); ND medium to large and KD medium, with mean values of 13.7 mm and 11.4 mm respectively; FA medium (mean = 20.9°); AA medium to large (mean = 16.2°). Bottom of ventral fissure straight.

Dorso-lateral longitudinal depressions and dorso-lateral double furrows moderately developed. Guard surface smooth, sometimes with weakly defined vascular markings.

REMARKS: Most of the specimens with complete biometry of morphogroup H (referred here to *B. obtusa*) were referred by Schulz (1979) to *B. obtusa* (40 specimens including the holotype), and single specimens to *B. inflata* (2 specimens) and *B. pseudobtusa* (7 specimens including the holotype).

Within the stratigraphic range of *B. obtusa*, Schulz (1979) distinguished three stratigraphic forms: forma *anterior*, *media* and *posterior* (youngest), which suggests that this population was not statistically coherent and that its definition was very wide. This was proved by the investigation of the present author. From the population of *obtusa sensu* Schulz (1979) it was possible to distinguish well-defined forms like

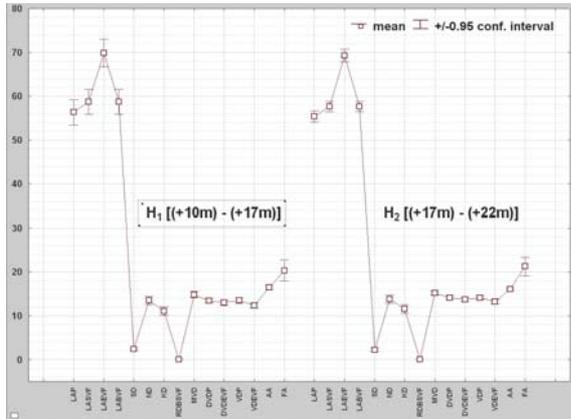
Belemnella sp. G, *Belemnella* sp. F and, in part, *B. vultensis*.

Additionally, the original diagnosis of *pseudobtusa*, included here into the synonymy, is confusing. According to it, *pseudobtusa sensu* Schulz (1979) is: 1) closely similar to *obtusa*; 2) occupies a different stratigraphic interval; and 3) differs in the ontogenetic development of the cross-section of the guard at the protoconch. The last criterion is invalid (compare the comments on the method of Schulz, above), since the cross-section of the guard is stable throughout the ontogeny; and the other two criteria are of no taxonomic value.

In conclusion, *B. obtusa* as understood here contains the holotypes and topotype material of both *B. obtusa* Schulz, 1979 and of *B. pseudobtusa* Schulz, 1979. As First Reviewer (Article 24.2.2 of ICZN Code), I include *B. pseudobtusa* into the synonymy of *B. obtusa* as understood here and interpret all the specimens of morphogroup H as representing *B. obtusa*.

The population of *B. obtusa* as herein defined is different from that of Schulz, being morphologically very stable throughout the entire stratigraphic range that it occupies. Moreover, no evolutionary changes were observed in the population of *B. obtusa* as understood herein (Text-fig. 29).

B. obtusa sensu Schulz (1979) has also been reported by Christensen (1999) from the Mons Basin, Belgium. This population was compared with *B. obtusa* as understood here (Text-fig. 30) but only on the basis of the six available mean values reported by Christensen (1999) and the herein calculated 95% confidence intervals: LAP = 56.3+/-4.01; SD = 2.2+/-0.4; DVDP = 15.2+/-1.07; VDP = 15.2+/-1.03; AA = 16.7+/-0.54; FA = 22.8+/-4.01. Based on such characteristics it can be concluded that this population may well represent *B. obtusa* as understood here (Text-fig. 30), suggesting an



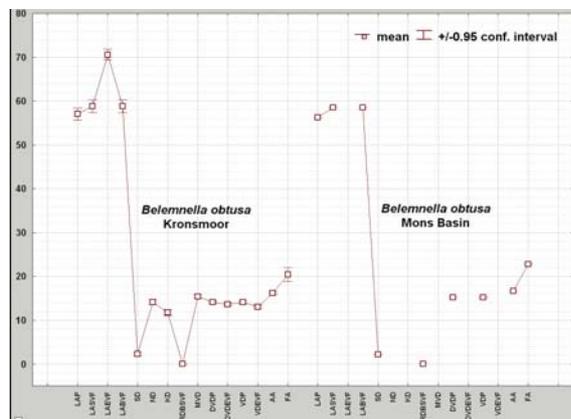
Text-fig. 29. Means and 95 % confidential intervals of features in the sub-group H_1 and H_2 from different stratigraphic intervals of Krons Moor

Early Maastrichtian age [Tercis definition] of the relevant stratigraphic interval in the Mons Basin.

The differences between *B. obtusa* and *Belemnella vistulensis* are relatively small; The latter is characterized by a very large FA (Text-fig. 25).

B. obtusa differs from *Belemnella* sp. G in significantly smaller values of length-features and diameters. *Belemnella* sp. G is characterized by slightly smaller values of SD and AA (Text-fig. 25). Compared with *Belemnella* sp. F, it possesses significantly higher values of LAEVP and FA; the SD, ND and KD are markedly larger in *Belemnella* sp. F (Text-fig. 25).

OCCURRENCE: In the Vistula section, *Belemnella obtusa* is known from the upper part of the Podole and Kłudzie S sections, most probably close to or above the “boundary marls”, and from the sections of Przedmieście and Dziurków. It is known from the interval +10.2 m to +25 m of Krons Moor, and from the Mons Basin, Belgium. The species is exclusively Early Maastrichtian [Tercis definition].



Text-fig. 30. Comparison of populations of *B. obtusa* [= morphogroup H] from Krons Moor and a sample [= *B. obtusa*] from the Mons Basin (data of Christensen 1999)

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PLATE 1

Belemnella longissima Schulz, 1979

- 1 – KK524; [= *B. longissima* in: Schulz, 1979]; level mB607 +/- 0.1m
- 2 – KK 408; [holotype of *B. longissima sensu* Schulz, 1979]; level mB/G606 + 0.6m
- 3 – KK 214; [= *B. inflata* in: Schulz, 1979]; level mB606 – 0.3m
- 4 – KK 625; [= *B. lanceolata* in: Schulz, 1979]; level mB606 + 1.5m
- 5 – S/BI46; [= *B. lanceolata* in: Schulz, 1979]; level 0m to 0.5m above the base of the Maastrichtian Balsvik, Schonen
- 6 – KK 609; [= *B. inflata* in: Schulz, 1979]; level mB606 + 1.6m
- 7 – KJ 201; [= *B. lanceolata* in: Schulz, 1979]; level F600 + 1.5m = mB602–1m
- 8 – RajN/060; section Raj N
- 9 – KłodzieN/005; section Kłodzie N
- 10 – RajN/016; section Raj N

a – ventral view; b – dorso-ventral view and the inner structure of the guard;

all specimens are $\times 1$

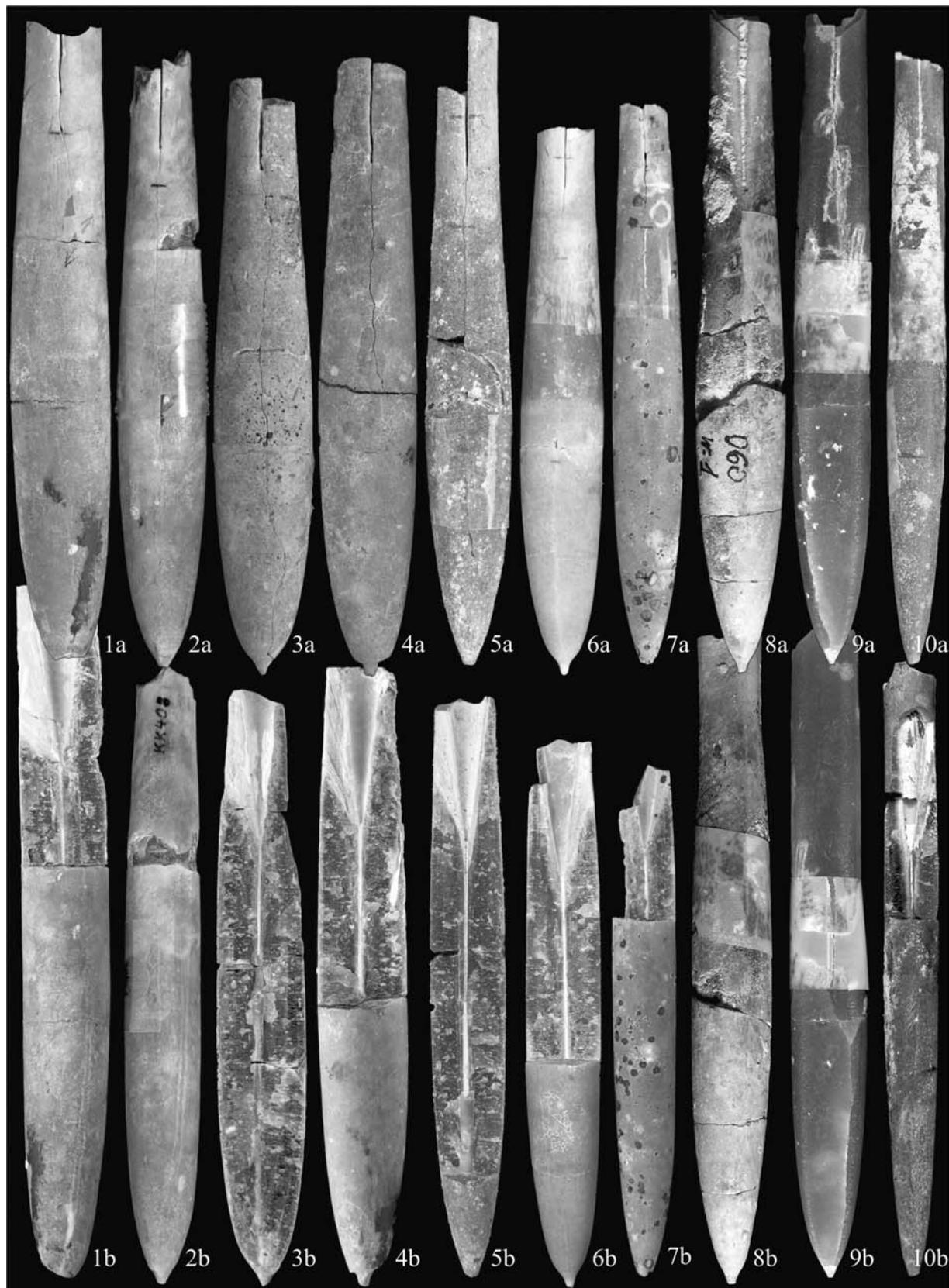


PLATE 2

Belemnella sp. A

- 1 – KK 220; [= *B. inflata* in: Schulz, 1979]; level mB606 – 0.1m
- 2 – KK 428; [= *B. inflata* in: Schulz, 1979]; level mB607 – 0.2m
- 3 – KK 207; [= *B. inflata* in: Schulz, 1979]; level 604 to 607 + 0.5m
- 4 – KK 105; [= *B. inflata* in: Schulz, 1979]; level mB606 – 0.55m
- 5 – KK 704; [= *B. inflata* in: Schulz, 1979]; level mB606 + 2.2m
- 6 – KK 533; [= *B. inflata* in: Schulz, 1979]; level mB606 + 1m to 1.5m
- 7 – KK 001; [= *B. inflata* in: Schulz, 1979]; level mB606-1,3m = mB605-ca.0,2m
- 8 – RajN/009; section Raj N

a – ventral view; b – dorso-ventral view and the inner structure of the guard;

all specimens are $\times 1$

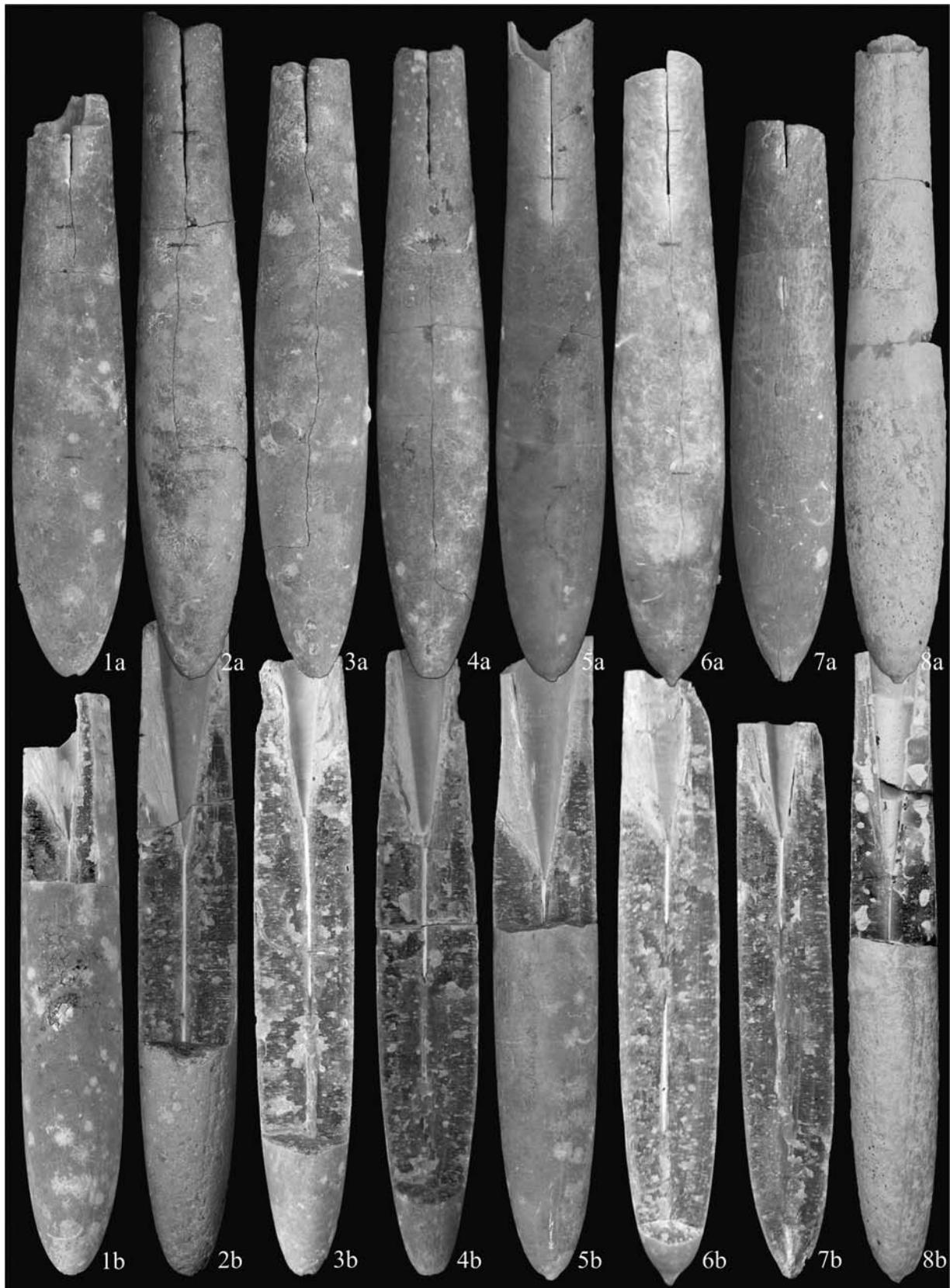


PLATE 3

Belemnella sp. G

- 1 – KM 811; [= *B. obtusa* in: Schulz, 1979]; level Gb616 + 2.3m
- 2 – KM 923; [= *B. obtusa* in: Schulz, 1979]; level G615 + 2.5 to 3m
- 3 – KM 301; [= *B. obtusa* in: Schulz, 1979]; level G615 – 0.1m
- 4 – KM 511; [= *B. obtusa* in: Schulz, 1979]; level G620 – 6m to 7m
- 5 – KM 002; [= *B. obtusa* in: Schulz, 1979]; level G615 – 1.3m to 1.4m
- 6 – KM 107; [= *B. obtusa* in: Schulz, 1979]; level G610 + 2 to 3m
- 7 – KM 516; [= *B. obtusa* in: Schulz, 1979]; level G615 + 0.8m
- 8 – KM 702; [= *B. obtusa* in: Schulz, 1979]; level G615 + 2m

a – ventral view; b – dorso-ventral view and the inner structure of the guard;

all specimens are $\times 1$



PLATE 4

Belemnella sp. F

- 1 – KM 829; [= *B. obtusa* in: Schulz, 1979]; level G615 + 2.5m [type]
- 2 – KM 618; [= *B. obtusa* in: Schulz, 1979]; level G620 – 5m to 7m
- 3 – KM 830; [= *B. obtusa* in: Schulz, 1979]; level G615 + 2.5m
- 4 – KM 909; [= *B. obtusa* in: Schulz, 1979]; level Gb616 + 2.5m to 3m
- 5 – KM 903; [= *B. obtusa* in: Schulz, 1979]; level G615 + 2.5 to 3.5m
- 6 – KM 712; [= *B. obtusa* in: Schulz, 1979]; level G615 + 2m
- 7 – KM 405; [= *B. obtusa* in: Schulz, 1979]; level G615 + 0.3m
- 8 – KM 601; [= *B. obtusa* in: Schulz, 1979]; level G615 + 1.6m
- 9 – KM 606; [= *B. obtusa* in: Schulz, 1979]; level G616 + 0.5m to 1.5m

a – ventral view; b – dorso-ventral view and the inner structure of the guard;

all specimens are $\times 1$

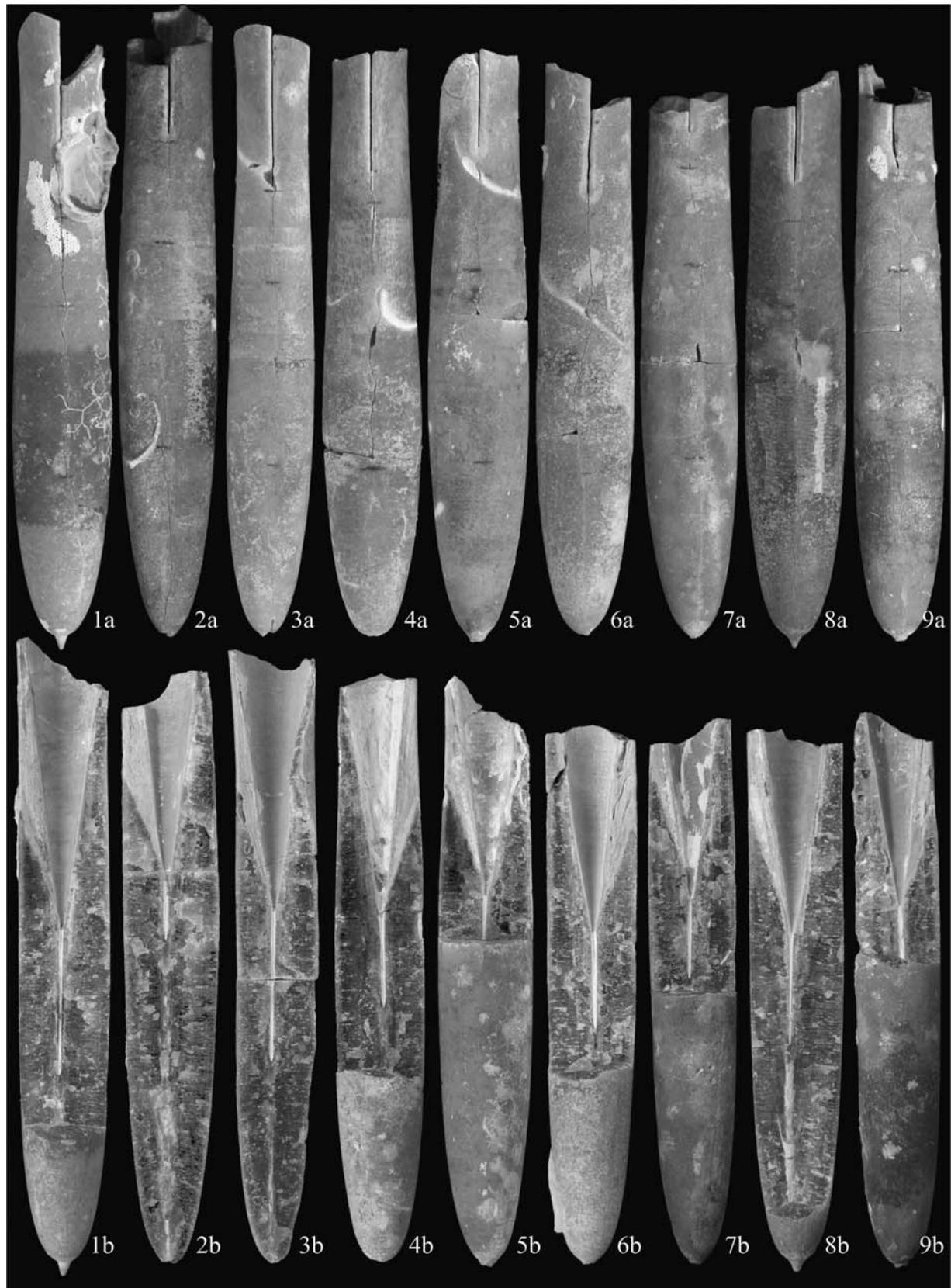


PLATE 5

Belemnella sp. C

- 1 – KK 521; [= *B. inflata* in: Schulz, 1979]; level mB607 +/- 0.3m
- 2 – KK 222; [= *B. inflata* in: Schulz, 1979]; level mB606 – 0.4m
- 3 – KK 008; [= *B. inflata* in: Schulz, 1979]; level mB605 – 0.3m = 603/(4) + 1m
- 4 – KK 706; [= *B. inflata* in: Schulz, 1979]; level mB606 + 2m
- 5 – KK 532; [= *B. inflata* in: Schulz, 1979]; level mB606 + 1.1m
- 6 – KK 215; [= *B. inflata* in: Schulz, 1979]; level mB605 to 607
- 7 – KJ 910; [= *B. inflata* in: Schulz, 1979]; level from G604 to mB605

a – ventral view; b – dorso-ventral view and the inner structure of the guard;

all specimens are $\times 1$

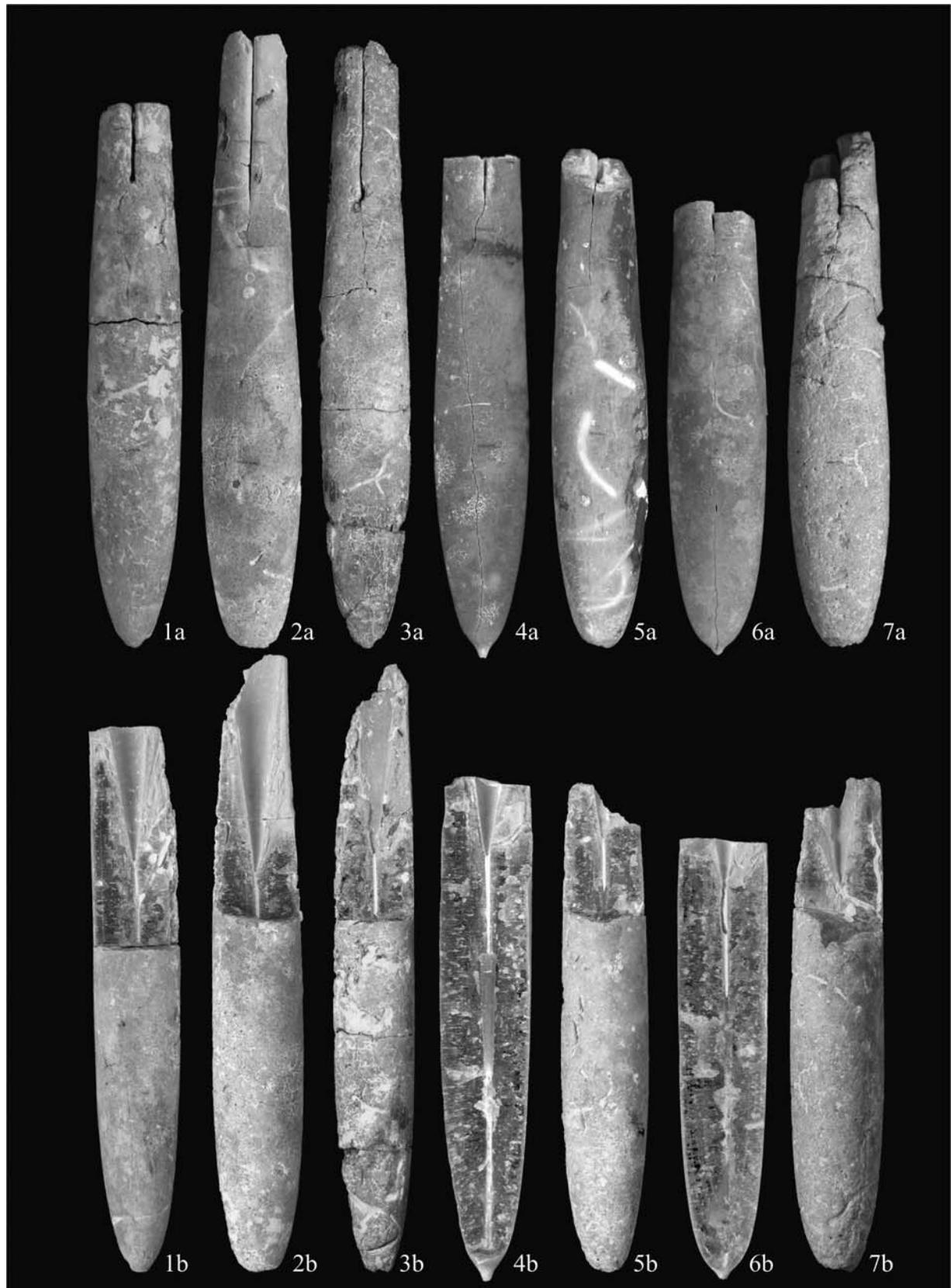


PLATE 6

Belemnella lanceolata (Schlotheim, 1813)

- 1 – KK 007; [= *B. obtusa* in: Schulz, 1979]; level G604 + 0.7m
- 2 – KK 102; [= *B. inflata* in: Schulz, 1979]; level mB605 – 0.5m to + 1m
- 3 – KK 708; [= *B. pseudobtusa* in: Schulz, 1979]; level mB607 + 1m
- 4 – S/BI 23; [= *B. inflata* in: Schulz, 1979]; level from 0m to 0.5m above the base of the Maastrichtian, Balsvik, Schonen
- 5 – S/BJ 24; [= *B. lanceolata sensu* Schulz, 1979; pl. 1, fig. 1]; level 0.5m above the base of the Maastrichtian, Balsvik, Schonen
- 6 – Raj/081; section Raj
- 7 – Raj N/027; section Raj N
- 8 – Raj N/040; section Raj N
- 9 – Raj N/050; section Raj N
- 10 – Kłodz N/008; section Kłodzie N
- 11 – Kłodz N/009; section Kłodzie N

a – ventral view; b – dorso-ventral view and the inner structure of the guard;

all specimens are $\times 1$

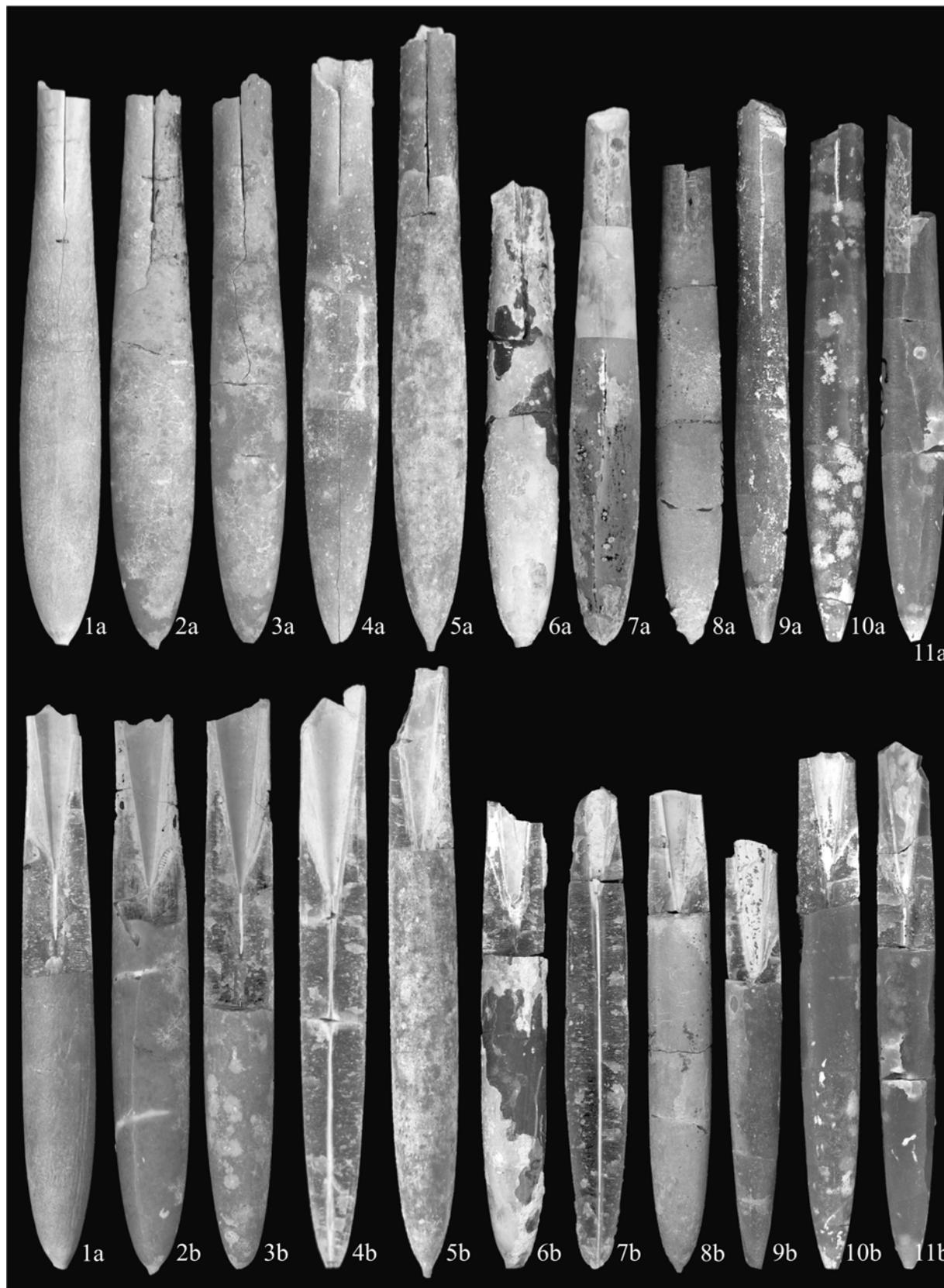


PLATE 7

Belemnella inflata (Arkhangelsky, 1912)

- 1 – KK 009; [= *B. inflata* in: Schulz, 1979]; level mB605 – 0.35m
- 2 – KK 803; [= *B. inflata* in: Schulz, 1979]; level mB606 + 2m to 3m
- 3 – KK 010; [= *B. inflata* in: Schulz, 1979]; level mB605 – 0.3m = 603/(4) + 1m
- 4 – KK 212; [= *B. inflata* in: Schulz, 1979]; level mB606 – 0.3m
- 5 – KK 903; [= *B. inflata* in: Schulz, 1979]; level mB607 + 0m to 4m
- 6 – KK 201; [= *B. inflata* in: Schulz, 1979]; level mB606 – 0.1m
- 7 – Raj N/001; section Raj N
- 8 – Raj N/051; section Raj N

a – ventral view; b – dorso-ventral view and the inner structure of the guard;

all specimens are $\times 1$

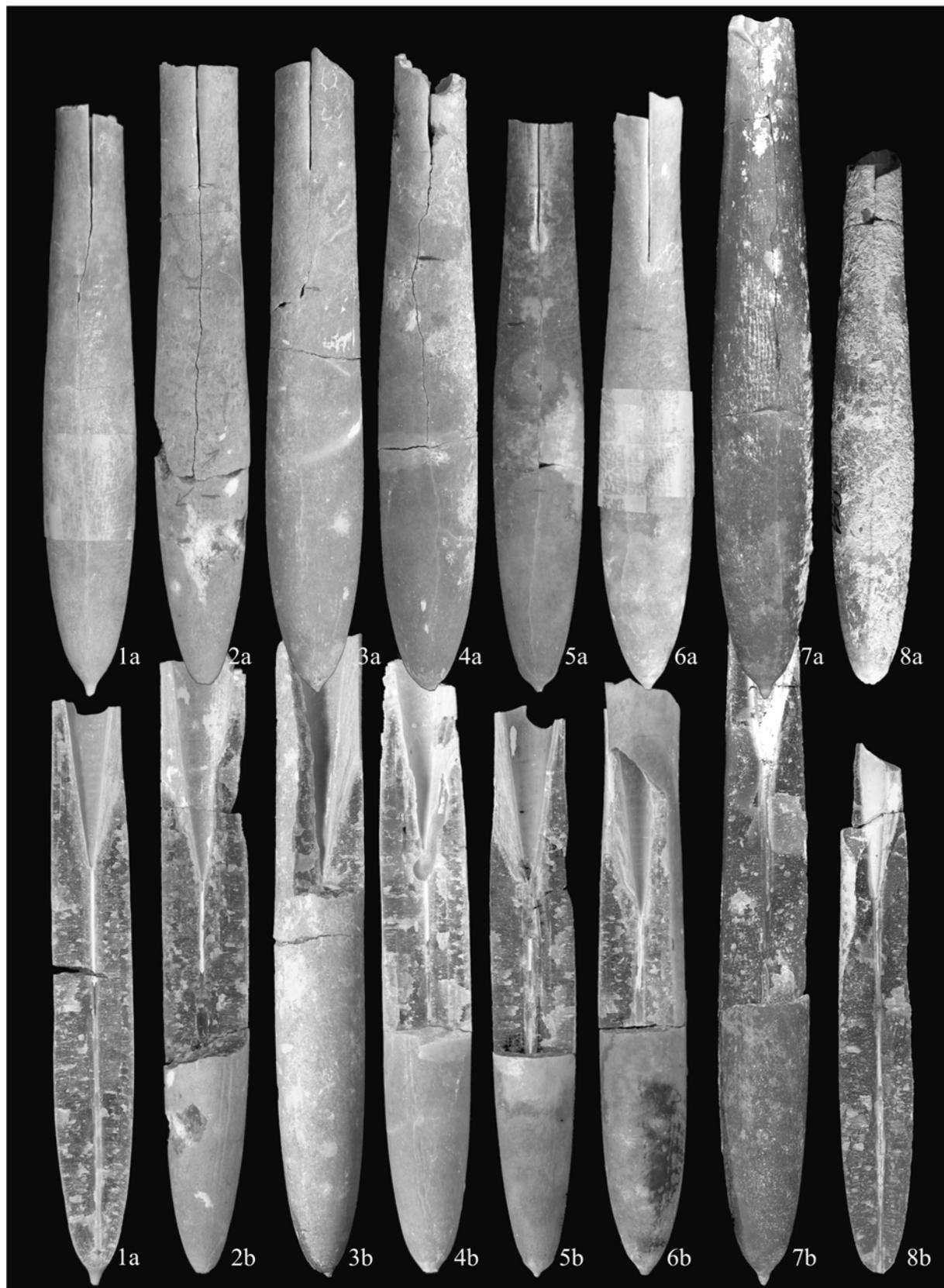


PLATE 8

Belemnella vistulensis (Kongiel, 1962)

- 1 – KM 312; [= *B. obtusa* in: Schulz, 1979]; level G615 – 0.25m
- 2 – KL 904; [= *B. inflata* in: Schulz, 1979]; level G610 – 1m
- 3 – KL 102; [= *B. pseudobtusa* in: Schulz, 1979]; level G610 – 2.2m
- 4 – KL 609; [= *B. inflata* in: Schulz, 1979]; level G610 + 0.2m
- 5 – KM 011; [= *B. obtusa* in: Schulz, 1979]; level G615 – 1.3 to 1.5m
- 6 – KłodzS/002; section Kłodzie S
- 7 – KłodzS/005; section Kłodzie S
- 8 – Przed/001; section Przedmieście
- 9 – Przed/002; section Przedmieście
- 10 – Dziu/016; section Dziurków
- 11 – Mcd190; holotype of *Belemnella vistulensis* (Kongiel, 1962); section Kłodzie
- 12 – Mcd191; paratype of *Belemnella vistulensis* (Kongiel, 1962); section Przedmieście

a – ventral view; b – dorso-ventral view and the inner structure of the guard;

all specimens are $\times 1$

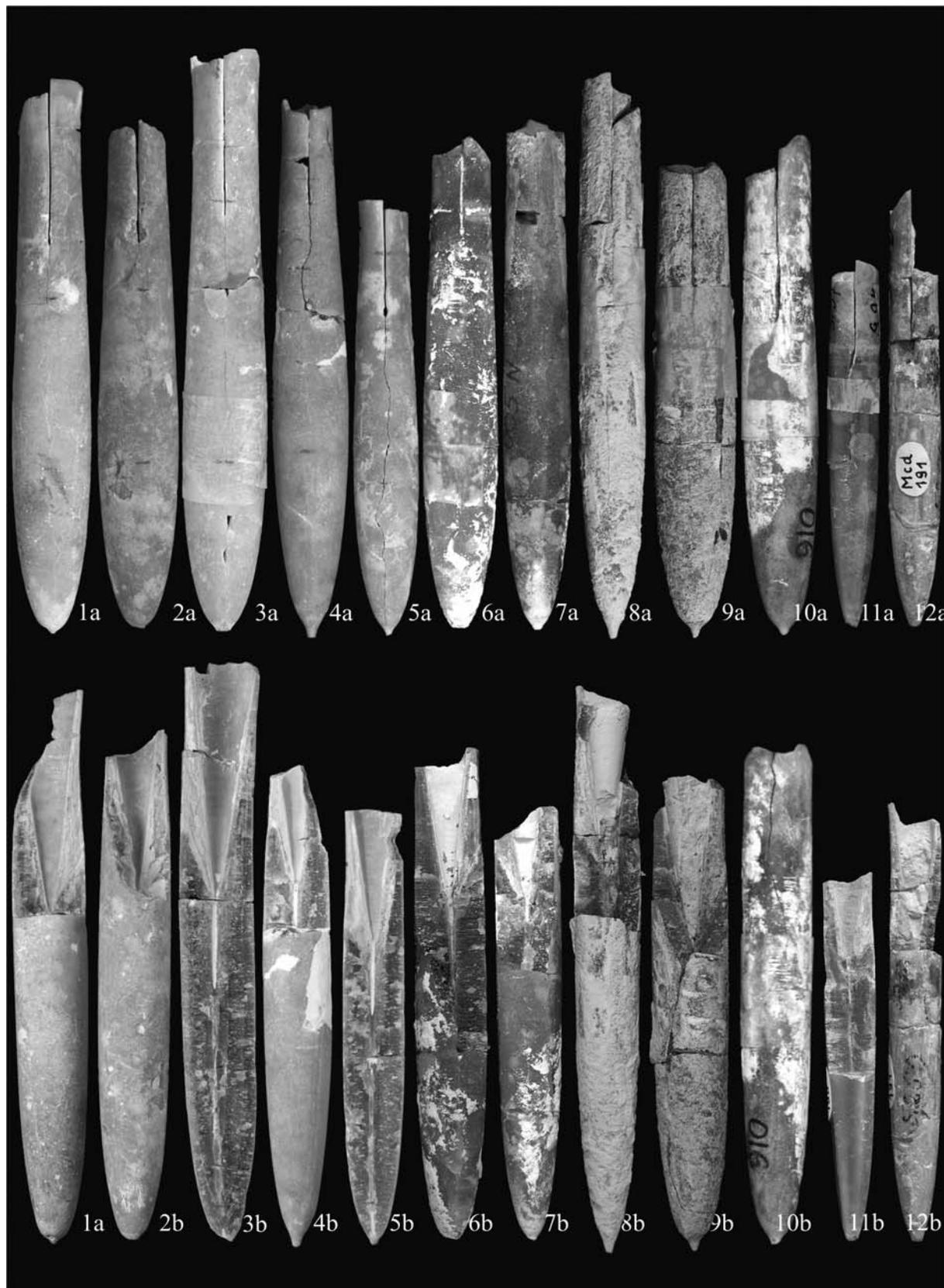


PLATE 9

Belemnella obtusa Schulz, 1979

- 1 – KN 810; [= holotype of *Belemnella obtusa* Schulz, 1979; pl. 9, figs. 3, 4]; level G620
- 2 – KM 823; [= *B. obtusa* in: Schulz, 1979]; level G615 + 1m to 4m
- 3 – KN 802; [= *B. obtusa* in: Schulz, 1979]; level G620 – 0.2m
- 4 – KM 815; [= *B. obtusa* in: Schulz, 1979]; level G615 + 2.2m to 2.5m
- 5 – KM 802; [= *B. obtusa* in: Schulz, 1979]; level G615 + 2m do 2.5m
- 6 – KM 609; [= *B. obtusa* in: Schulz, 1979]; level G615 + 1.3m
- 7 – Podole/030; section Podole
- 8 – Przed/009; section Przedmieście
- 9 – Dziu/020; section Dziurków

a – ventral view; b – dorso-ventral view and the inner structure of the guard;

all specimens are $\times 1$

