

Gradualistic evolution in *Belemnitella* from the middle Campanian of Lower Saxony, NW Germany

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Nine samples of the *Belemnitella* lineage, including the uppermost Lower and lower Upper Campanian *B. mucronata* and the uppermost lower Upper Campanian *B. misburgensis* sp. nov., from the expanded uppermost Lower and lower Upper Campanian succession of the Lehrte West Syncline east of Hannover, Lower Saxony, northern Germany have been subjected to univariate and bivariate statistical analyses. The succession consists of monotonous marly limestones and calcareous marls, which were deposited during 4–5 m.y. in a fairly stable environment. Based on superficial resemblance alone the nine samples are nearly identical, but trends have been recognized in the morphological characters when treated quantitatively. Three characters, the length from the apex to the protoconch, the slenderness of the guard and the alveolar angle, show evolutionary reversals (so-called zig-zag evolution) with net decreases or increases. The Schatzky distance shows stasis in *B. mucronata* and decreases in *B. misburgensis* sp. nov. The fissure angle displays unidirectional evolution and increases gradually. These morphological changes are interpreted as long term phyletic gradualism, although this model of evolution has almost universally been depicted as one of unidirectional change. *B. misburgensis* sp. nov. is closely allied to *B. mucronata* (its ancestor), but differs in its slightly smaller and more slender guard, in addition to its smaller Schatzky distance and larger fissure angle. *B. praecursor* is recorded from the uppermost five metres of the Lower Campanian, and this is the first record of this species from the highest Lower Campanian of northern Germany. The uppermost Lower and Lower Upper Campanian belemnite assemblages of the Misburg/Höver area in northern Germany are reviewed. The Upper Campanian *Belemnitella* successions of Norfolk in England, the Maastricht-Liège district in The Netherlands and Belgium, the Mons Basin in southern Belgium, Scania in southern Sweden and the Misburg-Höver area in northwest Germany are compared and contrasted.

Key words: Belemnites, *Belemnitella praecursor*, *B. mucronata*, *B. misburgensis* sp. nov., Campanian, Lehrte West Syncline, Lower Saxony, northwest Germany, biometry, gradualistic evolution, Upper Campanian *Belemnitella* successions.

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During the Early Campanian the *Goniotenthis* belemnite stock dominated in the Central European Subprovince and the *Belemnitella* stock characterized the Central Russian Subprovince. These subprovinces belonged to the North European palaeobiogeographical Province, as did the Baltoscandian Subprovince (Christensen 1997b) (Fig. 1). However, the last subprovince has been recognized only in the uppermost Lower Campanian and the lowermost Upper Campanian. It was characterized by the genus *Belemnellocomax* Naidin: *B. mammillatus* (Nilsson) in the uppermost Lower Campanian and *B. balsvikensis* (Brotzen) in the lowermost Upper Campanian. The Central European and Central Russian Subprovinces disappeared in the Upper Campanian, because the genus *Goniotenthis* Bayle became extinct at the bound-

ary between the Lower and Upper Campanian; the genus *Belemnitella* d'Orbigny expanded its area of distribution to cover the entire North European Province in the Upper Campanian, except Baltoscandia in the lowermost Upper Campanian.

It appears that species of the *Belemnitella* stock attempted to invade the Central European and Baltoscandian Subprovinces three times during the Early Campanian: *B. alpha* Naidin and *B. praecursor* Stolley in the lowest Lower Campanian, *B. praecursor* in the middle Lower Campanian, and *B. mucronata* (Schlotheim) in the uppermost Lower Campanian (Christensen 1997b). However, there was a third *B. praecursor* invasion (see below).

Northwest Germany belonged to the Central European Subprovince in the Lower Campanian, be-

cause *Goniatheuthis* Bayle predominated (Christensen 1997a, 1997b). However, mixed *Goniatheuthis/Belemnitella* assemblages have been recorded from the lowest and uppermost Lower Campanian. *B. praecursor* has been reported from lowest Lower Campanian *granulataquadrata* and *lingua/quadrata* Zones, viz. in marls at Braunschweig (Ernst 1964b, 1968), in the chalk of the Lägerdorf standard section in Schleswig-Holstein (Ernst 1964b) and in the Stromberg beds in the eastern part of the Münsterland Basin (Kaplan et al. 1996). The lower Lower Campanian *B. alpha*, 'B. aff. *mucronata/praecursor*' and 'B. aff. *senior/praecursor*' were reported from the Bottrop Marl in the southwestern part of the Münsterland Basin (Ernst 1964b, Christensen 1986, 1991).

Belemnitella was virtually absent in the middle part of the Lower Campanian of northwest Germany, that is a period of c. 2 m.y. A single specimen of *B. praecursor* was reported from the middle Lower Campanian *senonensis* Zone of Lägerdorf (Christensen & Schmid 1987).

Northwest Germany was reinvaded by *Belemnitella mucronata* in the uppermost Lower Campanian, where it co-occurred with *Goniatheuthis quadrata gracilis* (Stolley) in the *gracilis/mucronata* Zone.

It was assumed previously that *Belemnitella praecursor*

disappeared in the middle Lower Campanian and was replaced by *B. mucronata* in the uppermost Lower Campanian in northern Germany. However, three specimens of *B. praecursor* are recorded here from the upper part of the *gracilis/mucronata* Zone of the Germania IV quarry at Misburg.

The aim of the present paper is to analyze the morphological trends in the genus *Belemnitella*, including *B. mucronata* and *B. misburgensis* sp. nov., from the expanded uppermost Lower and lower Upper Campanian succession, consisting of monotonous marly limestones and calcareous marls, of the Misburg/Höver area east of Hannover in the Lehrte West Syncline, Lower Saxony (Fig. 2). These species are described below, as is *B. praecursor*. Moreover, the uppermost Lower and lower Upper Campanian belemnite assemblages of northern Germany are reviewed, and Upper Campanian *Belemnitella* zonation of northwest Europe are compared and discussed.

Material

The belemnites examined during the course of the present study were collected by the author, the late

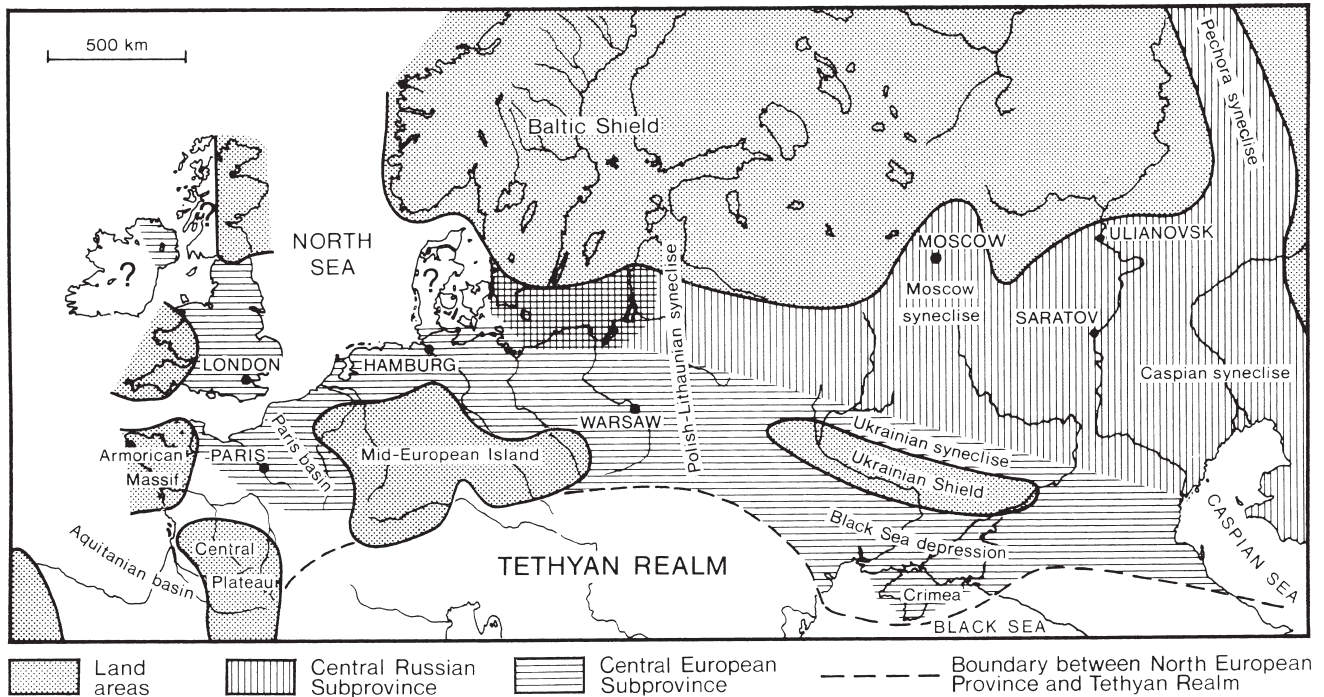


Fig. 1. Map showing the Central European and Central Russian Subprovinces of the North European palaeobiogeographical Province, as defined by the *Goniatheuthis* and *Goniocamax-Belemnitella* stocks, respectively (modified from Christensen 1976). The Baltoscandian Subprovince (indicated by crosshatching) is distinguished by the genus *Belemnelloamax* in the uppermost Lower and lowest Upper Campanian. Upper Cretaceous land and sea areas represent maximum inundation for all stages. The boundaries are not reliable in detail and the biogeographical units are typically gradational in character.

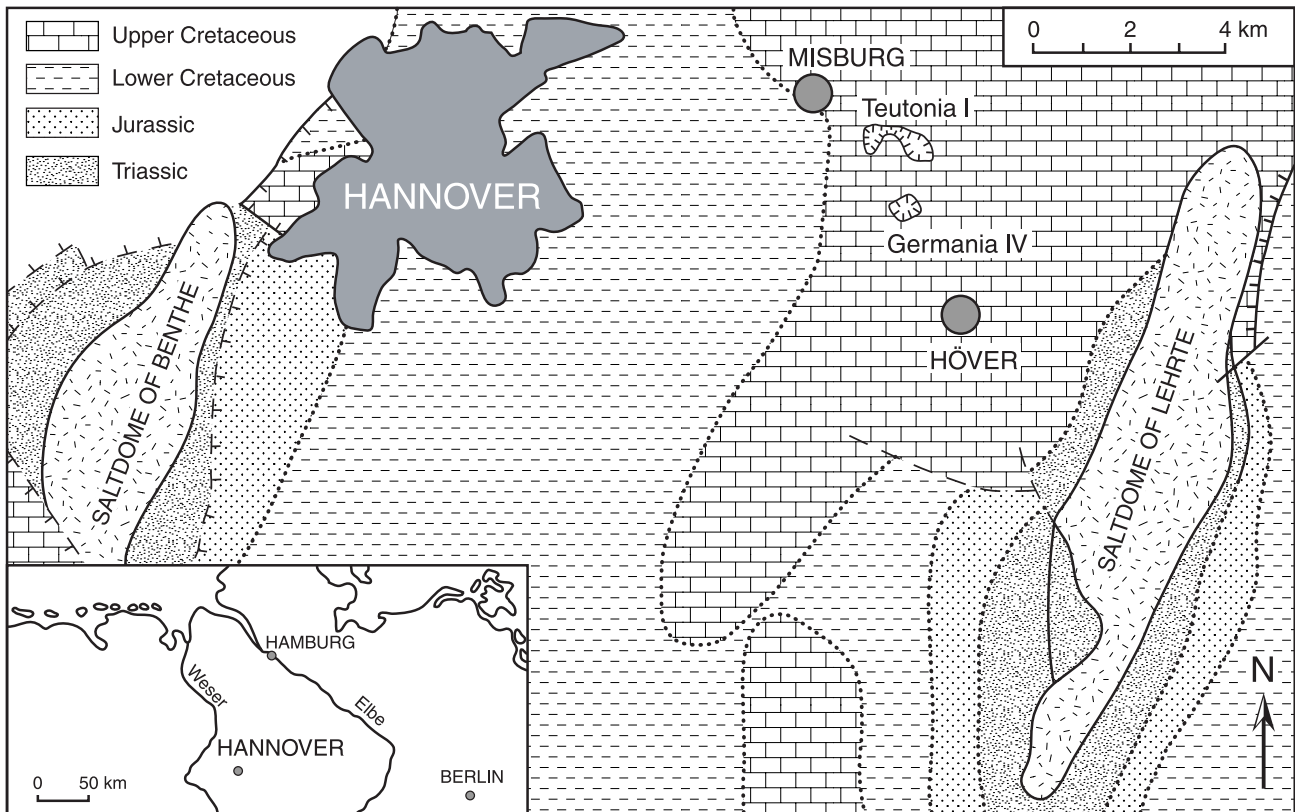


Fig. 2. Map of the Lehrte West Syncline east of Hannover, showing the location of the Germania IV and Teutonia I quarries. Modified from Christensen et al. (1975).

Dr M.-G. Schulz (Kiel) and Mr S.L. Jakobsen (Copenhagen) during field work in 1975–1977. The material consists of c. 700 specimens, which are housed in the Geological Museum, University of Copenhagen. It should be noted, however, that only 54% of the specimens could be split in the median plane. Consequently, the internal characters are known only in approximately half of the specimens.

In addition, the results of a biometric analysis by Christensen et al. (1975) of a sample consisting of 132 specimens of *Belemnitella mucronata* from the middle part of the *stobaei/basiplana* Zone of the Germania IV quarry (sample GR, see below) are included in this paper. Ten specimens, including all growth stages, were figured by Christensen et al. (1975). An adult specimen from this sample was proposed as neotype for *B. mucronata* by Christensen et al. (1975) and was later designated as neotype for that species by the International Commission on Zoological Nomenclature (1985, Opinion 1328). This sample is housed in the Niedersächsisches Landesamt für Bodenforschung, Hannover, Germany.

Figured specimens are housed in the Type Collection of the Geological Museum, with prefix MGUH.

Geological setting

The upper Lower and lower Upper Campanian succession of the Misburg-Höver area, east of Hannover, in the Lehrte West Syncline consist of ca. 350 m of monotonous calcareous marls and marly limestones (Abu-Maaruf 1973, 1975; Ernst 1963b, 1968, 1976; Ernst et al. 1979, 1997a, 1997b; Khosrovschahian 1972; Niebuhr 1995, Rehfeld et al. 1998). The succession was subdivided into approximately 200 beds by Khosrovschahian (1972) and Abu-Maaruf (1973, 1975) and these were numbered and used as a basic framework for fossil collecting.

The calcareous marls and marly limestones alternations have been interpreted as climatically controlled cycles, reflecting orbital forcing in the Milankovitch frequency band (Niebuhr & Prokoph 1997, Rehfeld et al. 1998, Niebuhr 1999).

Sedimentary and biostratonomic evidence indicates that this succession does not show any sign of interruptions, and actual non-sequences can be excluded from consideration (Christensen et al. 1975). Calcareous, nodular concretions, containing calcified tissues of siliceous demosponges, have been reported from the succession (Ernst et al. 1997a, Rehfeld et al.

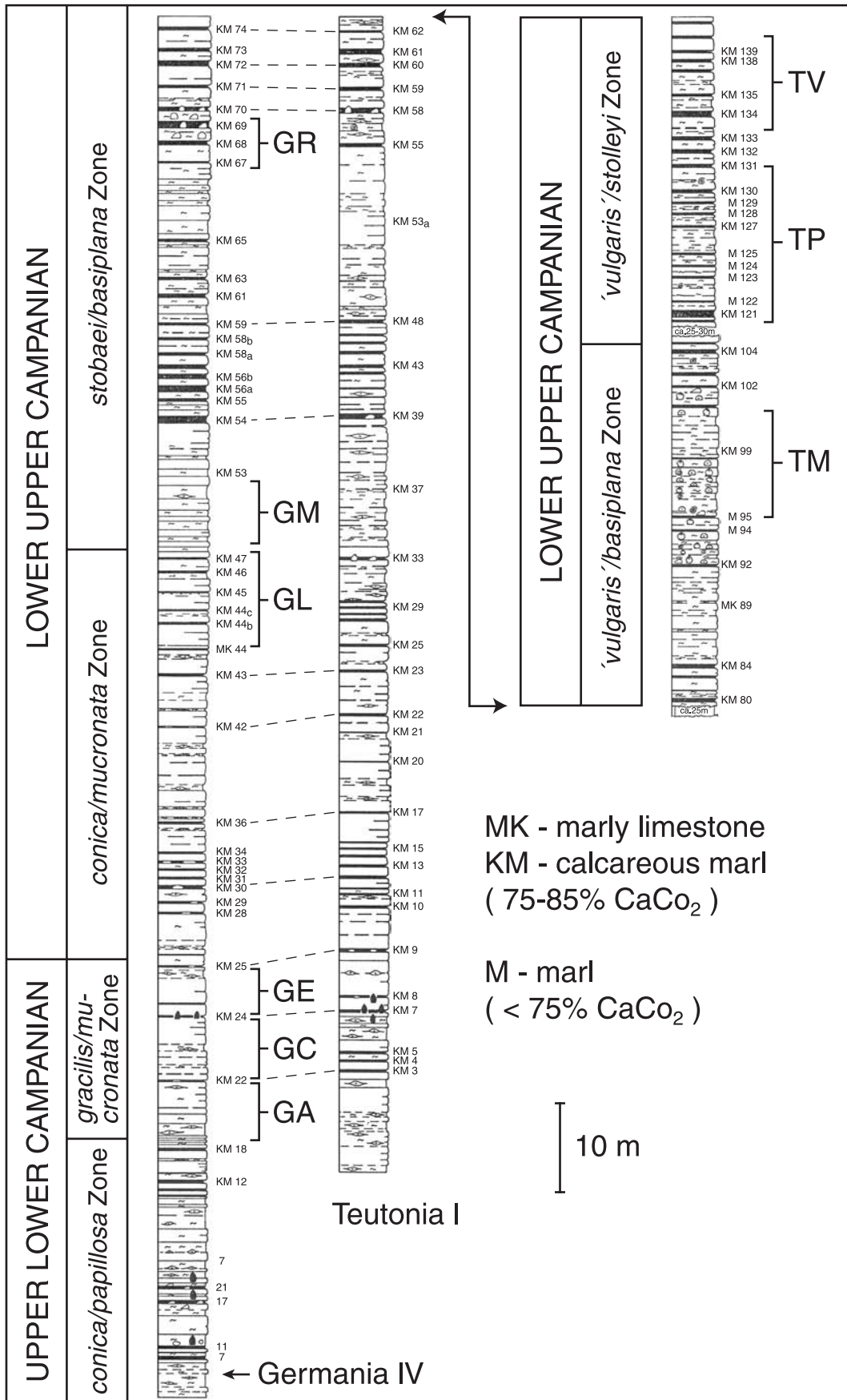


Fig. 3. Stratigraphy of the samples of *Belemnites* from the Campanian of the Germania IV and Teutonia I quarries. Logs and stratigraphy after Ernst (1976) using data from Khosrovschahian (1972) and Abu-Maaruf (1973, 1975). MK - 'Mergelkalk' (marly limestone); KM - 'Mergelkalk' (calcareous marl).

CHRONO-STRATIGR.	BIOZONATION, NW GERMANY				Range of belemnites, NW Germany
	MISBURG-HÖVER			LÄGERDORF	
	1	2	3	4	
LOWER UPPER CAMPANIAN	upper <i>vulgaris</i> Subzone	<i>vulgaris</i> Subzone	' <i>vulgaris</i> '/ <i>stolleyi</i> Zone	<i>roemeri</i> Zone	
	<i>vulgaris/basiplana</i> Subzone	<i>vulgaris/basiplana</i> Subzone	' <i>vulgaris</i> '/ <i>basiplana</i> Zone	<i>basiplana/spiniger</i> Zone	
	upper <i>conicus/senior</i> Subzone	<i>stobaei/basiplana</i> Subzone	<i>stobaei/basiplana</i> Zone		
	lower <i>conicus/senior</i> Subzone	<i>conica/senior</i> Subzone	<i>conica/mucronata</i> Zone	<i>conica/senior</i> Zone	
UPPER LOWER CAMPANIAN	<i>gracilis/senior</i> Zone	<i>gracilis/senior</i> Subzone	<i>gracilis/mucronata</i> Zone	<i>gracilis/senior</i> Zone	
	<i>conicus/papillosa</i> Zone	<i>conica/papillosa</i> Subzone	<i>conica/papillosa</i> Zone	<i>conica/gracilis</i> Zone	
	<i>papillosa</i> Zone		<i>papillosa</i> Zone	<i>papillosa</i> Zone	
	<i>senonensis</i> Subzone		<i>senonensis</i> Zone	<i>senonensis</i> Zone	
	<i>pilula/senonensis</i> Subzone		<i>pilula/senonensis</i> Zone	<i>pilula/senonensis</i> Zone	

Fig. 4. Stratigraphical diagram, showing the zonation of the upper Lower and lower Upper Campanian of the Misburg-Höver area and Lägerdorf in northwest Germany and range of belemnites. *B.* – *Belemnellocomax*; *Blt.* – *Belemitella*; *G.* – *Goniot euthis*. Sources: column 1, Ernst (1963b, 1968); column 2, Khosrovschahian (1972), column 3, Niebuhr et al. (1997) and Ernst et al. (1997a, 1997b); column 4, Schulz et al. (1984) and Schulz (1996); column 5, Ernst (1963a, 1963b, 1964a), Christensen & Schulz (1976), Christensen & Schmid (1987), and Christensen (this paper and unpublished). The single specimen of *B. praecursor* from the *senonensis* Zone of Lägerdorf recorded by Christensen & Schmid (1987) is plotted in the middle part of the zone.

1998). These concretions probably indicate reduced sedimentation rates during the time of their formation.

The succession of the Germania IV quarry is about 140 m thick, comprises approximately 75 beds, and includes the upper Lower Campanian *conica/papillosa* and *gracilis/mucronata* Zones, in addition to the lower Upper Campanian *conica/mucronata* and *stobaei/basiplana* Zones (Khosrovschahian 1972, Ernst 1976, Ernst et al. 1997a) (Fig. 3). The succession of the Teutonia I quarry is a little less than 250 m thick, comprises approximately 141 beds, and includes the upper Lower Campanian *conica/papillosa* and *gracilis/mucronata* Zones, in addition to the lower Upper Campanian *conica/mucronata*, *stobaei/basiplana*, '*vulgaris*'/*basiplana* and '*vulgaris*'/*stolleyi* Zones (Khosrovschahian 1972, Ernst 1976, Ernst et al. 1997b) (Fig. 3). Thus, the lower part of the succession exposed in the Teutonia I quarry equates with the main part of the succession exposed in the Germania IV quarry (Khosrovschahian 1972, Ernst 1976). The uppermost Lower and lower Upper Campanian zones are discussed below.

In 1991 the Teutonia I quarry was enlarged and the lower part of the upper Upper Campanian *minor/polyplocum* Zone became exposed (Niebuhr 1996, Niebuhr et al. 1997, Ernst et al. 1997b, Rehfeld et al. 1998).

Stratigraphy

At the Brussels Symposium on Cretaceous Stage Boundaries in 1995, it was provisionally recommended that the boundary marker for the base of the Campanian should be placed at the extinction level of the crinoid *Marsupites testudinarius* Schlotheim, which is compatible with the first occurrence of the ammonite *Placenticerias bidorsatum* (Roemer), the classic definition by de Grossouvre (1901) (Hancock & Gale 1996). In northwest Germany, the extinction level of *Marsupites* equates with the first evolutionary occurrence of the belemnite *Goniot euthis granulataquadrata* (Stolley) (Ernst 1963a, 1966, 1968). It was also endeavoured to subdivide the stage into three substages, Lower, Middle and Upper, but it was not possible at that time to make formal definitions for the bases of the Middle and Upper Campanian.

Following the suggestion by Jeletzky (1958, pp. 47–48) many authors in Europe have subdivided the Campanian into two substages, Lower and Upper. The base of the Campanian was placed at the first occurrence of *Placenticerias bidorsatum* and the extinction level of *Marsupites*. The base of the Upper Campanian was taken at the first occurrence of the am-

monites *Hoplitoplacenticeras coesfeldiense* (Schlüter) and *Neancyloceras phaleratum* (Griepenkerl) and the extinction level of the genus *Goniot euthis*, and not at the first occurrence of *Belemnitella mucronata* (Schlotheim). The *Goniot euthis quadrata gracilis/Belemnitella mucronata* Zone of Ernst (1963a, 1963b, 1976) and Ernst et al. (1979) (= 'Overlap Zone' of Schmid 1953, 1955, 1956) is thus the uppermost belemnite zone of the Lower Campanian (Fig. 4).

The Campanian of the USA has been subdivided into three substages, Lower, Middle and Upper, by Cobban (1994). The Lower Campanian of the USA corresponds approximately to the European Lower Campanian, and hence the Middle and Upper Campanian of the USA equate with the European Upper Campanian.

The uppermost Lower and lower Upper Campanian succession of the Misburg-Höver area in the Lehrte West Syncline were subdivided into one zone, followed by four subzones by Ernst (1963b, 1968) (Fig. 4). The upper *conicus/senior* Subzone of Ernst was renamed the *stobaei/basiplana* Subzone by Khosrovschahian (1972), and the upper *vulgaris* Subzone of Ernst (= *vulgaris* Subzone of Khosrovschahian) was renamed the '*vulgaris/stolleyi* Zone by Niebuhr et al. (1997) (Fig. 4). The lower Upper Campanian zones were treated as zones by Ernst et al. (1997a, 1997b).

The *gracilis/mucronata* Zone is a concurrent range zone. The base is defined by the first occurrence of *Belemnitella mucronata* and the top by the last occurrence of *Goniot euthis quadrata gracilis*. Khosrovschahian (1972) placed the base of this zone within bed MK21 in the Germania IV quarry. However, *B. mucronata* has been found 1.3 m below the base of the *gracilis/mucronata* Zone of Khosrovschahian, and the zone should thus be extended downwards by 1.3 m.

The four lower Upper Campanian zones are based on cephalopods and irregular echinoids, and each of the zones is characterized by two index fossils. However, the zones were not clearly defined by Ernst (1963b, 1968, 1976) and Khosrovschahian (1972).

The base of the *conica/mucronata* Zone is defined by the last occurrence of *Goniot euthis quadrata gracilis* and the top by the last occurrence of *Echinocorys* ex gr. *conica* (Agassiz). Both of the eponymous species occur in the subjacent *gracilis/mucronata* Zone and *B. mucronata* also occurs above the zone (Ernst et al. 1997a, 1997b).

The base of the *stobaei/basiplana* Zone is defined by the last occurrence of *Echinocorys* ex gr. *conica* and the top by the first occurrence of *Galerites* ex gr. *vulgaris* (Leske). The ammonite *Patagiosites stobaei* (Nilsson) has an acme in the lower half of the zone, but occurs both below and above the zone as does *Galeola papillosa basiplana* Ernst (Ernst et al. 1997a, 1997b).

The base of the '*vulgaris/basiplana* Zone is defined by the first occurrence of *Galerites* ex gr. *vulgaris* and the top is placed slightly below the last occurrence of *Galeola papillosa basiplana* (Ernst et al. 1997a, 1997b).

The base of the '*vulgaris/stolleyi* Zone is placed at the last occurrence of *Galeola papillosa basiplana* and the top by the occurrence of *Nostoceras polyplacum* (Roemer) (Niebuhr et al. 1997). However, it is worthy of note that Ernst et al. (1997a) recorded *G. papillosa basiplana* from the basal part of this zone.

The biozonation of the standard white chalk reference section of Lägerdorf-Kronsmoor-Hemmoor (Schulz 1996) is very closely similar to that of the Misburg-Höver area (Fig. 4), with two exceptions. Schulz (1985) replaced the *Galerites vulgaris* Zone of Misburg-Höver by the new *G. roemeri* Zone. According to Ernst et al. (1997b) this revision is not justified, because the stratum typicum and type locality of *G. roemeri* (Desor) is the middle upper Upper Campanian Opoka of Ahlten near Hannover. Moreover, Schulz (1985) substituted the *stobaei/basiplana* Zone with the *basiplana/spiniger* Zone, because *Patagiosites stobaei* appears in the uppermost Lower Campanian. The base of the *basiplana/spiniger* Zone is defined by the first occurrence of *Trachyscaphites spiniger* (Schlüter) and the last occurrence of *Echinocorys conica*, and the top by the last occurrence of *Galeola papillosa basiplana* and the first occurrence of *Galerites roemeri* Schulz (Schulz 1985). Schulz (1985, p. 41) also noted that the *basiplana/spiniger* Zone of Lägerdorf equated with the *stobaei/basiplana* and '*vulgaris/basiplana* Zones of Misburg-Höver. It should be noted, however, that Schulz (1996) later mentioned that the *basiplana spiniger* Zone corresponded only to the *stobaei/basiplana* Zone. This interpretation was also put forward by Niebuhr (1995) and Ernst et al. (1996).

The timespan of the Campanian Stage was long, about 12 m.y., and the duration of the Early Campanian was about 3 m.y., about one third of the length of the Late Campanian (Obradovich 1994).

The samples of *Belemnitella* analyzed biometrically in this paper came from the uppermost Lower and lower Upper Campanian *gracilis/mucronata*, *conica/mucronata*, *stobaei/basiplana*, '*vulgaris/basiplana* and '*vulgaris/stolleyi* Zones (Figs 3–4). The duration of these zones is estimated to have been 4–5 m.y.

Sequence stratigraphy. – Niebuhr et al. (1997) and Niebuhr (1999) have undertaken a sequence stratigraphical analysis of the Campanian of the Lehrte West Syncline. They recognized a single, long-lasting 3rd order cycle, the so-called Middle/Upper Campanian cycle of Niebuhr (1999), which started with the tectono-eustatically triggered *Belemnitella mucronata* transgression in the uppermost Lower Campanian

and ranged up to the *Bostrychoceras polyplacum* regression in the basal part of the upper Upper Campanian. The peak transgression lay in the middle part of the *stobaei/basiplana* Zone. Niebuhr et al. (1997) estimated the depth of the sea to have been c. 150 m during peak transgression.

The uppermost Lower and lower Upper Campanian belemnite succession of the Lehrte West Syncline

The belemnite assemblage of the uppermost Lower Campanian *gracilis/mucronata* Zone consisted of *Goniotentis quadrata gracilis*, *Belemnitella mucronata*, *Belemnitella praecursor*, here recorded for the first time, *Belemnelloccamax mammillatus* (Nilsson) and *Belemnelloccamax* ex gr. *gossouvrei* (Janet) (Fig. 4). *G. quadrata gracilis* and *B. mucronata* were common and all growth stages were represented. The frequency of *G. quadrata gracilis* decreased gradually upwards, whereas the frequency of *B. mucronata* peaked in the middle part of the zone (Khosrovschahian 1972). *Belemnelloccamax mammillatus* occurred very rarely (three adult specimens are at hand), whereas only one adult specimen of *B. ex gr. gossouvrei* has been collected (Christensen unpublished). The exact horizon within the *gracilis/mucronata* Zone of these four specimens is not known. In addition, three specimens of *Belemnitella praecursor* are recorded here from the uppermost five metres of the *gracilis/mucronata* Zone of the Germania IV quarry, between beds KM24 and KM25. These specimens are described below. I have examined altogether 134 specimens of *Belemnitella* from the entire *gracilis/mucronata* Zone of the Germania IV quarry and *B. praecursor* occurred only in the upper five metres of the zone. Therefore, the occurrence of *B. praecursor* was probably due to a migration into the Misburg-Höver area from elsewhere, probably the Russian Platform. *Belemnelloccamax mammillatus* probably migrated southwards to the Misburg-Höver area from Scania in southern Sweden (Christensen 1997b).

The belemnite assemblage of the basal Upper Campanian *conica/mucronata* Zone comprised *Belemnitella mucronata* and very rare *Belemnelloccamax balsvikensis*. In fact, only two specimens of *B. balsvikensis* have been recorded; both of these came from the top of the zone in the Germania IV quarry (Christensen & Schulz 1976). One is juvenile and the other is adolescent. The latter probably migrated southwards to the Misburg-Höver area from Scania (Christensen 1997b). The pres-

ence of the juvenile specimen at Misburg is an enigma, since it is very unlikely that the distance from Scania to the Misburg-Höver area, c. 500 km, could have been covered by active swimming. Christensen & Schulz (1976) suggested, therefore, that it may have drifted to the Misburg-Höver area during heavy storms, either as a gas-filled carcass or clinging to driftwood or sea-weed.

The belemnite assemblages of the superjacent lower Upper Campanian zones were monospecific. *Belemnitella mucronata* occurred in the *stobaei/basiplana* and '*vulgaris*'/*basiplana* Zones and in the lower part of the '*vulgaris*'/*stolleyi* Zone, whereas only *B. misburgensis* sp. nov. occurred in the upper part of the '*vulgaris*'/*stolleyi* Zone (see below).

It is worthy of note, however, that Niebuhr et al. (1997) recorded *B. woodi* Christensen from the '*vulgaris*'/*stolleyi* Zone. Ernst et al. (1997b, p. 94) reported a large species of *Belemnitella*, tentatively assigned to *B. woodi*, from the '*vulgaris*'/*stolleyi* Zone and small transitional forms with a large fissure angle from the upper part of the zone. These were referred to as *B. minor sensu germanico*. I regard these determinations as open to question and suspect that they should be placed in *B. misburgensis* sp. nov.

Since *Belemnitella* was common in the uppermost Lower and lower Upper Campanian succession of Misburg-Höver and all growth stages were represented it seems that the genus bred and spawned there.

Methods of study

The following standard characters of Christensen (1995) were measured: length from apex to protoconch (LAP), dorsoventral diameter at protoconch (DVDP), lateral diameter at protoconch (LDP), maximum lateral diameter (MLD), Schatzky distance (SD), fissure angle (FA), and alveolar angle (AA) (Fig. 5). Measurements are in mm and degrees. Linear measurements were made with a vernier calliper to an accuracy of 0.1 mm, and angles were measured with a goniometer fitted on a Wild stereomicroscope to an accuracy of 0.5°.

The Birkelund Index (BI) is the length from the apex to the protoconch divided by the dorsoventral diameter at the protoconch (Christensen 1995).

Christensen (1995) introduced a classification of the size of species of *Belemnitella* based on the length from the apex to the protoconch. This is as follows: 1) guard small, LAP less than 55 mm; 2) guard large, LAP 55–65 mm; 3) guard very large, LAP larger than 65 mm. He also introduced a classification of the slenderness

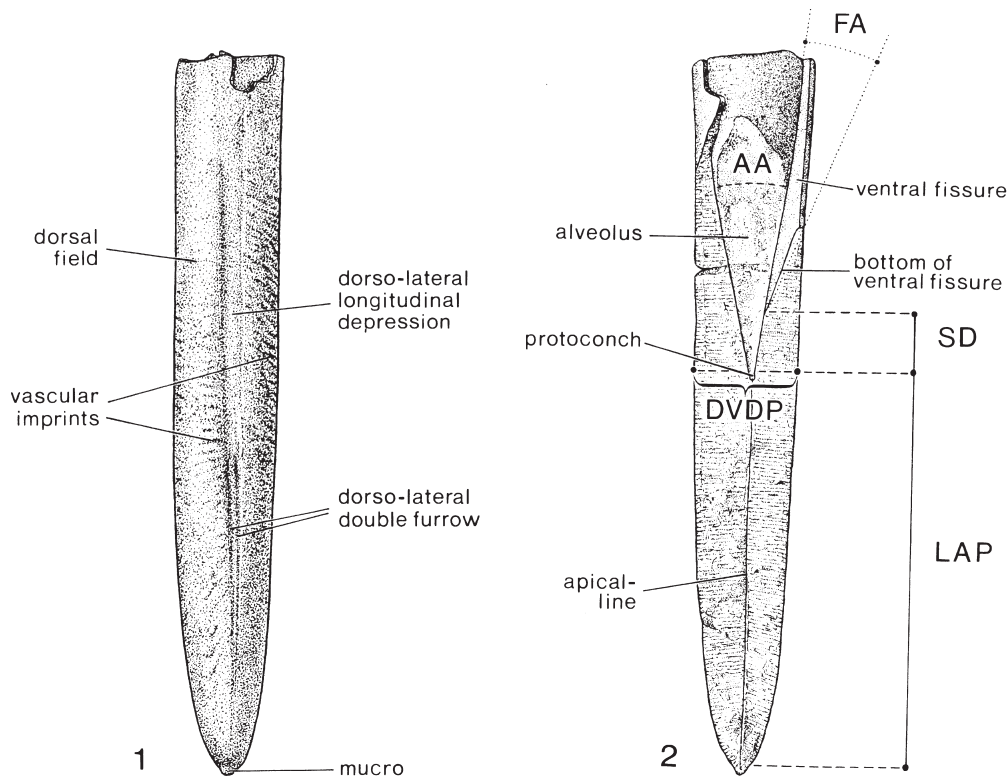


Fig. 5. Morphological elements of the guard; neotype of *Belemnitella mucronata*. 1, ventrolateral view; 2, view of the split guard. LAP – length from apex to protoconch; DVDP – dorsoventral diameter at protoconch; SD – Schatzky distance; FA – fissure angle; AA – alveolar angle. After Christensen (1975).

of the guard based on the mean value of the Birke-lund Index. This is as follows: 1) guard stout, mean value of the BI less than 4; 2) guard slender, mean value of the BI 4–5; 3) guard very slender, mean value of the BI larger than 5.

Species variation was analyzed using univariate and bivariate statistical methods and is summarized by descriptive statistics, histograms and scatter diagrams.

In the univariate analyses the estimates of the following statistics were calculated: the arithmetical mean value (\bar{X}), standard deviation (s), and coefficient of variation (CV). In addition, the observed range (OR) is reported, and N is the number of specimens. Size-frequency distributions were tested for normality using the powerful non-parametric Kolmogorov-Smirnov test for goodness of fit.

The regression line is written $y = a + bx$, and the original measurements were used in the calculations, because of the linear trend on ordinary graph paper and the homoscedastic variance of the regression line. Estimates of the following statistics were calculated: the slope (b) and standard deviation of the slope (s_b); the intercept on the y -axis (a) and the standard deviation of the intercept (s_a); the standard deviation of the

regression line ($s_{y,x}$); and the correlation coefficient (r). N is the number of specimens. The correlation coefficients were tested for significance using Table Y in Rohlf & Sokal (1969), and t -tests on the y -intercepts are performed in order to see if the intercepts differ significantly from zero. The latter test has significant biological implications, because a regression line passing through the origin indicates isometric growth, $y = bx$. Regression lines of two samples were compared in the way described by Hald (1957, pp. 571–579).

Conventional statistical significance levels are as follows:

0.05 > P > 0.01; significant*
 0.01 > P > 0.001; highly significant**
 P < 0.001; very highly significant***; P = probability.

Biometric analysis

Nine samples of *Belemnitella* were analyzed biometrically, six from the Germania IV quarry (prefix G) and three from the Teutonia I quarry (prefix T) (Fig. 3).

The samples were collected from stratigraphical intervals of varying thickness (see below). It is worthy of note that the samples consist of growth-series containing all growth stages and represent an accumulation of several generations.

The stratigraphy of the samples is as follows, in ascending stratigraphical order (Fig. 3).

- 1 Sample GA was collected from the basal 4 m of the *gracilis/mucronata* Zone, from bed KM 19 to immediately below MK 22.
- 2 Sample GC was collected from a 3.4 m interval in the middle part of the *gracilis/mucronata* Zone, from bed KM 22 to immediately below bed MK 24.
- 3 Sample GE came from the uppermost 5.3 m of the *gracilis/mucronata* Zone, from bed KM 24 to bed KM 25.
- 4 Sample GL came from the uppermost 9 m of the *conica/mucronata* Zone, from immediately above bed MK 44 to immediately above bed KM 47.
- 5 Sample GM came from the basal 6.5 m of the *stobaei/basiplana* Zone, from immediately above bed KM 47 to the top of bed MK 52b.
- 6 Sample GR came from a 4.6 m interval in the middle part of the *stobaei/basiplana* Zone, from immediately below bed KM 67 to immediately above bed KM 69 (see Christensen et al. 1975).
- 7 Sample TM came from a c. 10 m interval in the upper part of the '*vulgaris*'/*basiplana* Zone, from bed M 95 to immediately below bed bed MK 101.
- 8 Sample TP came from a 15 m interval in the lower part of the '*vulgaris*'/*stolleyi* Zone, from bed KM 120 to bed MK 131.
- 9 Sample TV came from a 10 m interval in the upper part of the '*vulgaris*'/*stolleyi* Zone, from immediately above bed M 133 to bed KM 140. The latter bed is c. 12 m below the top of the lower Upper Campanian.

Samples GA to TP are placed in *Belemnitella mucronata*, whereas sample TV is assigned to *B. misburgensis* sp. nov. for reasons given below.

Univariate analyses were made for all samples; bivariate analyses of the length from the apex to the protoconch *vs* the dorsoventral diameter at the protoconch were made only for samples GE-TV, due to the small number of specimens in samples GA and GC.

Univariate analysis

The results of the univariate analyses are shown in Tables 1–9. Histograms of the length from the apex to

the protoconch, Birkelund Index, Schatzky distance, fissure angle, and alveolar angle of samples GE-TV are shown in Figure 6. Histograms of samples GA and GC are not included due to the small number of specimens in these samples.

The histogram of the Birkelund Index of sample TV is two-topped, and the histogram of the fissure angle of sample TP is strongly right-skewed. These were tested for normality using the Kolmogorov-Smirnov test, and the tests showed that the size-frequency distributions did not differ significantly from normality at the 5% level.

Christensen et al. (1975) showed that the 'size'-characters in *Belemnitella mucronata* were very highly correlated, whereas the internal characters, that is the Schatzky distance, fissure angle and alveolar angle, were correlated neither with the 'size'-parameters nor with each other.

Christensen (1995) discussed the relative variability, as expressed by the coefficient of variation, of 43 samples of *Belemnitella*, representing 20 species and subspecies, including five samples of *B. mucronata* from the Germania IV quarry. He showed that the coefficients of variation of the standard characters

Table 1. Univariate analysis of *Belemnitella mucronata*, sample GA, lower part of the *gracilis/mucronata* Zone, Germania IV quarry.

Character	N	Univariate analysis:			
		\bar{X}	s	CV	OR
LAP	12	48.0	5.1	10.5	37.0–56.1
DVDP	12	14.1	1.8	13.0	10.3–17.4
LDP	12	14.3	2.0	14.2	10.1–18.5
MLD	10	14.4	1.1	7.8	13.1–16.3
SD	7	8.4	1.4	17.0	6.4– 9.7
FA	4	13.5	3.1	23.0	9.0–16.0
AA	6	20.4	0.8	3.9	19.0–21.0
BI	12	3.4	0.2	5.4	3.2– 3.7

Table 2. Univariate analysis of *Belemnitella mucronata*, sample GC, middle part of the *gracilis/mucronata* Zone, Germania IV quarry.

Character	N	Univariate analysis:			
		\bar{X}	s	CV	OR
LAP	22	47.8	6.4	13.5	35.0–58.1
DVDP	24	14.7	2.4	16.4	10.0–20.6
LDP	24	15.0	2.6	17.6	10.0–22.1
MLD	18	14.9	2.6	17.2	10.0–22.1
SD	15	7.7	1.8	23.6	4.8–11.0
FA	12	18.9	9.3	49.0	10.0–45.0
AA	17	20.2	1.0	4.9	18.0–22.0
BI	22	3.3	0.3	9.7	2.6– 3.7

Table 3. Univariate and bivariate analyses of *Belemnitella mucronata*, sample GE, upper part of the *gracilis/mucronata* Zone, Germania IV quarry.

Univariate analysis:					
Character	N	\bar{X}	s	CV	OR
LAP	38	45.2	6.3	14.0	29.0–61.8
DVDP	44	12.9	1.8	13.6	8.1–17.7
LDP	44	13.1	1.8	14.1	8.0–17.8
MLD	35	13.0	1.9	14.9	8.0–17.8
SD	34	7.9	1.7	21.2	5.3–11.3
FA	30	19.3	5.7	26.7	9.0–29.9
AA	33	20.4	0.8	3.8	19.0–21.5
BI	38	3.6	0.3	7.6	3.0– 4.1

Bivariate analysis:

DVDP = $1.9337 + 0.2396LAP$; $N = 38$; $r = 0.8450^{***}$;
 $s_a = 1.1428$; $s_b = 0.0251$; $s_{yx} = 1.1428$;
 $t_a = 1.6920$; $0.10 > P > 0.05$, with 36 degrees of freedom.

Table 4. Univariate and bivariate analyses of *Belemnitella mucronata*, sample GL, top of the *conica/mucronata* Zone, Germania IV quarry.

Univariate analysis:					
Character	N	\bar{X}	s	CV	OR
LAP	108	41.3	6.1	14.8	25.1–58.5
DVDP	107	13.0	2.2	17.1	7.7–18.2
LDP	102	13.1	2.5	19.0	6.9–18.8
MLD	83	13.6	2.2	16.3	7.9–18.8
SD	84	8.1	1.5	18.5	4.9–12.6
FA	80	18.9	5.5	5.5	5.5–32.0
AA	87	20.7	1.0	4.6	18.0–25.0
BI	108	3.2	0.3	10.5	2.5– 4.0

Bivariate analysis:

DVDP = $1.5352 + 0.2773LAP$; $N = 108$; $r = 0.7612^{***}$;
 $s_a = 0.9616$; $s_b = 0.0231$; $s_{yx} = 1.4461$;
 $t_a = 1.5964$; $0.20 > P > 0.10$, with 106 degrees of freedom.

Table 5. Univariate and bivariate analyses of *Belemnitella mucronata*, sample GM, basal part of the *stobaei/basiplana* Zone, Germania IV quarry.

Univariate analysis:					
Character	N	\bar{X}	s	CV	OR
LAP	78	43.2	6.8	15.8	25.6–56.0
DVDP	78	12.9	2.5	19.1	7.1–18.9
LDP	78	12.9	2.7	20.8	6.7–19.2
MLD	66	13.4	2.3	17.0	8.9–19.0
SD	67	7.7	1.5	19.2	4.3–12.3
FA	63	21.0	8.3	39.7	8.0–47.0
AA	69	20.6	1.1	5.1	18.5–24.0
BI	78	3.4	0.4	10.3	2.6– 4.3

Bivariate analysis:

DVDP = $-0.4238 + 0.3069LAP$; $N = 78$; $r = 0.8495^{***}$;
 $s_a = 0.9570$; $s_b = 0.0219$; $s_{yx} = 1.3985$;
 $t_a = 0.4429$; $0.70 > P > 0.60$, with 76 degrees of freedom.

Table 6. Univariate and bivariate analyses of *Belemnitella mucronata*, sample GR, middle part of the *stobaei/basiplana* Zone, Germania IV quarry. After Christensen et al. (1975).

Univariate analysis:					
Character	N	\bar{X}	s	CV	OR
LAP	89	43.1	7.1	16.5	20.5–57.8
DVDP	91	12.8	2.3	18.2	5.5–17.2
LDP	91	12.9	2.6	19.9	5.1–17.7
MLD	–	–	–	–	–
SD	77	7.7	1.9	24.5	4.5–14.7
FA	77	22.7	8.3	36.8	18.0–47.0
AA	85	19.6	1.1	5.4	18.0–21.5
BI	88	3.4	0.3	9.3	2.5– 4.4

Bivariate analysis:

DVDP = $0.5156 + 0.2800LAP$; $N = 88$; $r = 0.8654^{***}$;
 $s_a = 0.7741$; $s_b = 0.0177$; $s_{yx} = 1.1829$;
 $t_a = 0.6661$; $0.60 > P > 0.50$, with 86 degrees of freedom.

Table 7. Univariate and bivariate analyses of *Belemnitella mucronata*, sample TM, '*vulgaris*'/*basiplana* Zone, Teutonia I quarry. * – estimated.

Univariate analysis:					
Character	N	\bar{X}	s	CV	OR
LAP	46	45.2	4.9	10.9	35.8–58.3
DVDP	47	13.4	2.1	15.4	10.2–18.3
LDP	46	13.5	2.2	16.1	9.8–19.0
MLD	43	13.5	2.1	15.2	9.9–17.8
SD	38	7.6	1.3	16.5	4.9–10*
FA	38	23.6	8.1	34.3	10.0–49.0
AA	36	19.9	0.9	4.5	18.0–22.0
BI	46	3.4	0.3	9.3	2.6– 4.1

Bivariate analysis:

DVDP = $0.0019 + 0.2939LAP$; $N = 46$; $r = 0.7424^{***}$;
 $s_a = 1.7945$; $s_b = 0.0395$; $s_{yx} = 1.2988$;
 $t_a = 0.0011$; $P > 0.90$, with 44 degrees of freedom.

Table 8. Univariate and bivariate analyses of *Belemnitella mucronata*, sample TP, lower part of the '*vulgaris*'/*stolleyi* Zone, Teutonia I quarry.

Univariate analysis:					
Character	N	\bar{X}	s	CV	OR
LAP	43	42.6	6.2	14.6	26.5–55.9
DVDP	46	12.7	2.0	15.4	9.2–17.7
LDP	46	13.0	2.1	16.3	9.5–17.8
MLD	42	13.1	2.2	16.7	9.5–18.1
SD	36	7.8	1.3	16.2	5.6–10.8
FA	37	23.7	10.0	42.0	11.0–55.5
AA	36	19.0	0.7	3.8	18.0–20.5
BI	43	3.4	0.3	9.1	2.6– 4.1

Bivariate analysis:

DVDP = $1.5887 + 0.2597LAP$; $N = 43$; $r = 0.8105^{***}$;
 $s_a = 1.2170$; $s_b = 0.0289$; $s_{yx} = 1.1604$;
 $t_a = 1.3054$; $0.20 > P > 0.10$, with 41 degrees of freedom.

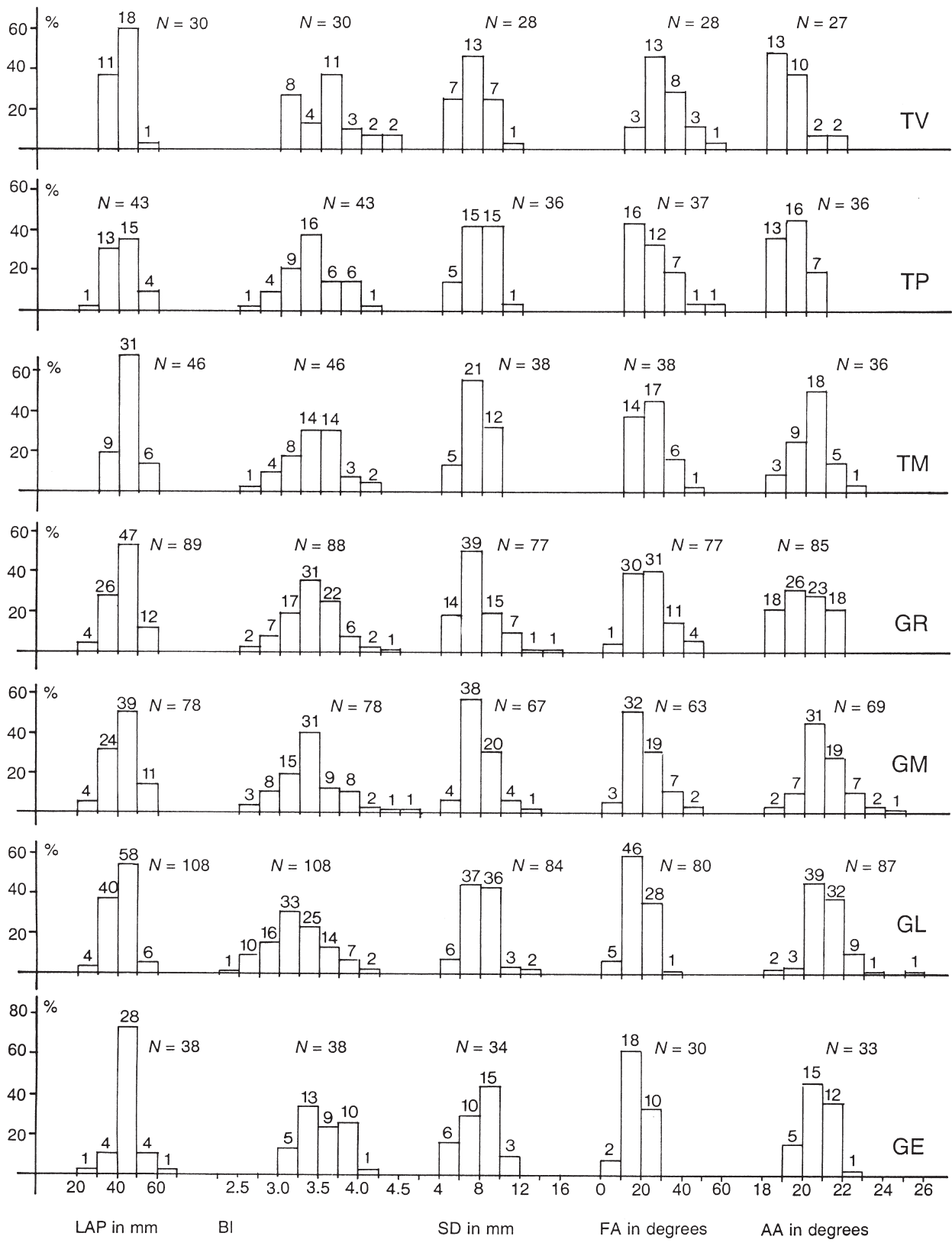


Fig. 6. Histograms of the length from the apex to the protoconch (LAP), Birkelund Index (BI), Schatzky distance (SD), fissure angle (FA) and alveolar angle (AA) of samples GE-GR from the Germania IV quarry and samples TM-TV from the Teutonia I quarry. The figures above the bars are the actual number of specimens. N = number of specimens.

Table 9. Univariate and bivariate analyses of *Belemnitella misburgensis* sp. nov., sample TV, upper part of the 'vulgaris'/stolleyi Zone, Teutonia I quarry.

Univariate analysis:					
Character	N	\bar{X}	s	CV	OR
LAP	30	41.8	5.3	12.8	31.3–53.4
DVDP	33	11.8	1.5	12.8	8.2–14.4
LDP	32	11.9	1.7	14.0	8.8–15.4
MLD	27	12.1	1.6	13.4	9.1–15.4
SD	28	7.2	1.5	21.5	4.1–10.6
FA	28	31.1	9.1	29.2	15.0–51.0
AA	27	18.8	0.9	5.0	18.0–21.0
BI	30	3.6	0.4	10.1	3.1– 4.4

Bivariate analysis:

DVDP = 2.8223 + 0.2130LAP; N = 30; r = 0.7293***;
 $s_a = 1.5853$; $s_b = 0.0376$; $s_{yx} = 1.0722$;
 $t_a = 1.7803$; $0.10 > P > 0.05$, with 28 degrees of freedom.

generally varied as shown in Table 10. Lower values were obtained in small samples, which did not reveal the entire variability.

The coefficients of variation of the length from the apex to the protoconch of the nine samples vary from 11 to 17 and thus fall within the relative variation as reported by Christensen (1995). The coefficients of variation of the Birkelund Index generally vary from 9 to 10 and are thus compatible with the relative variation as shown by Christensen (1995). A lower value was obtained in sample GA (CV = 5.4) and this is most likely due to the small number of specimens in this sample. The coefficients of variation of the Schatzky distance vary from 16–25 and thus fall within the relative variation as recorded by Christensen (1995). The coefficients of variation of the fissure angle vary from 25–50 and are thus compatible with those reported

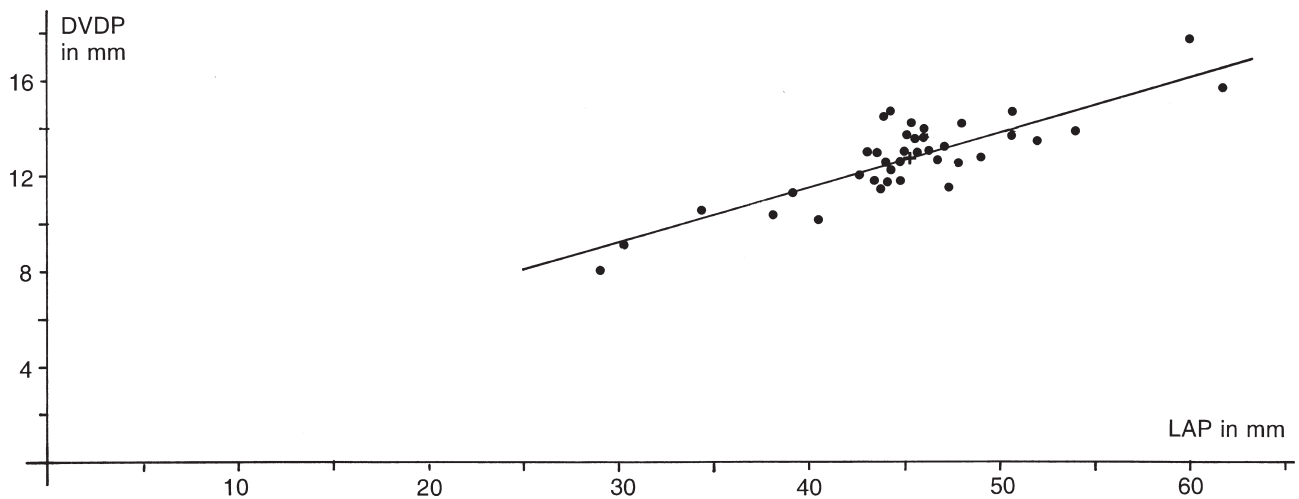


Fig. 7. Scatter plot and regression line of the length from the apex to the protoconch (LAP) vs the dorsoventral diameter at the protoconch (DVDP) of *Belemnitella mucronata* from sample GE, upper part of the *gracilis/mucronata* Zone of the Germania IV quarry.

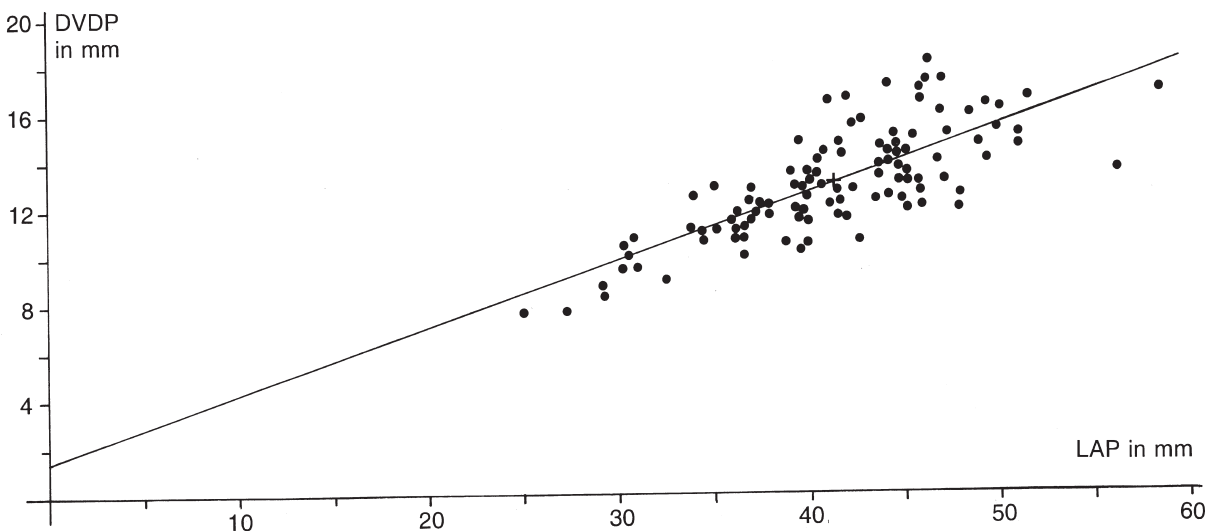


Fig. 8. Scatter plot and regression line of the length from the apex to the protoconch (LAP) vs the dorsoventral diameter at the protoconch (DVDP) of *Belemnitella mucronata* from sample GL, upper part of the *conica/mucronata* Zone of the Germania IV quarry.

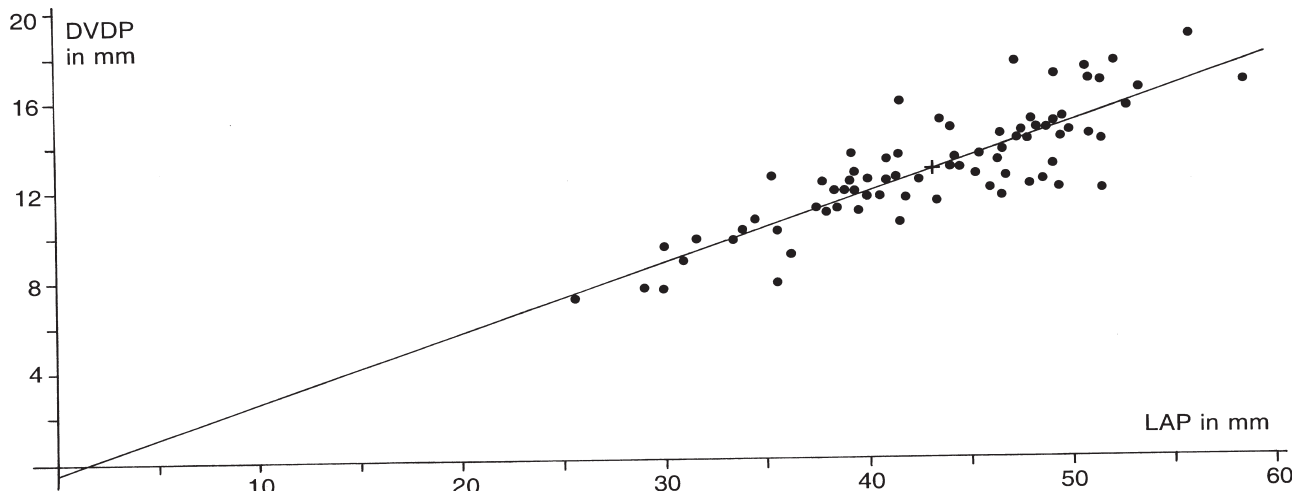


Fig. 9. Scatter plot and regression line of the length from the apex to the protoconch (LAP) vs the dorsoventral diameter at the protoconch (DVDP) of *Belemnitella mucronata* from sample GM, basal part of the *stobaei/basiplana* Zone of the Germania IV quarry.

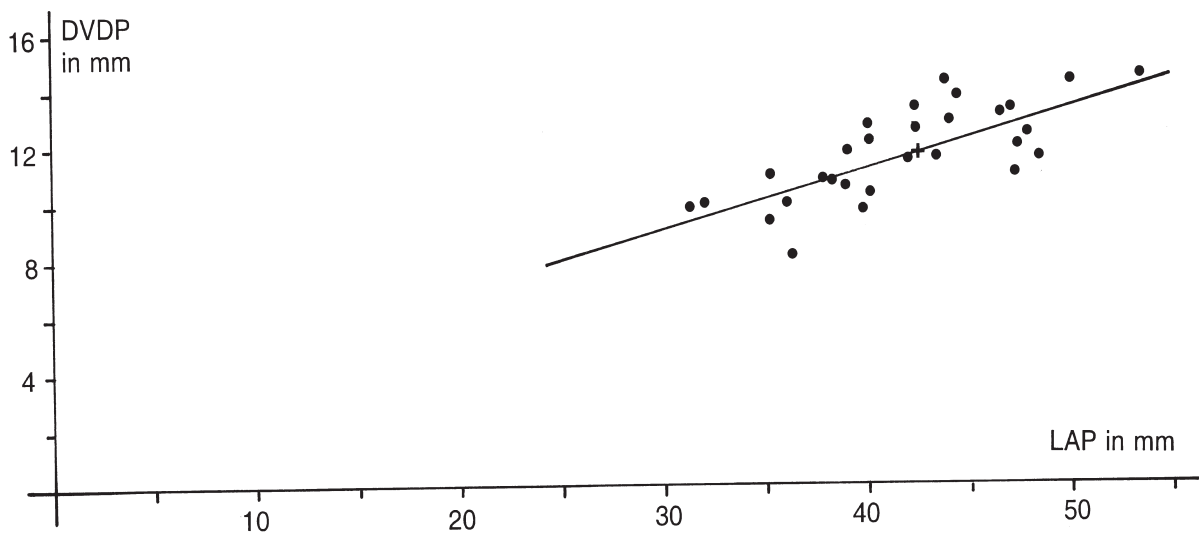


Fig. 10. Scatter plot and regression line of the length from the apex to the protoconch (LAP) vs the dorsoventral diameter at the protoconch (DVDP) of *Belemnitella misburgensis* sp. nov. from sample TV, upper part of the '*vulgaris*/'*stolleyi* Zone of the Teutonia I quarry.

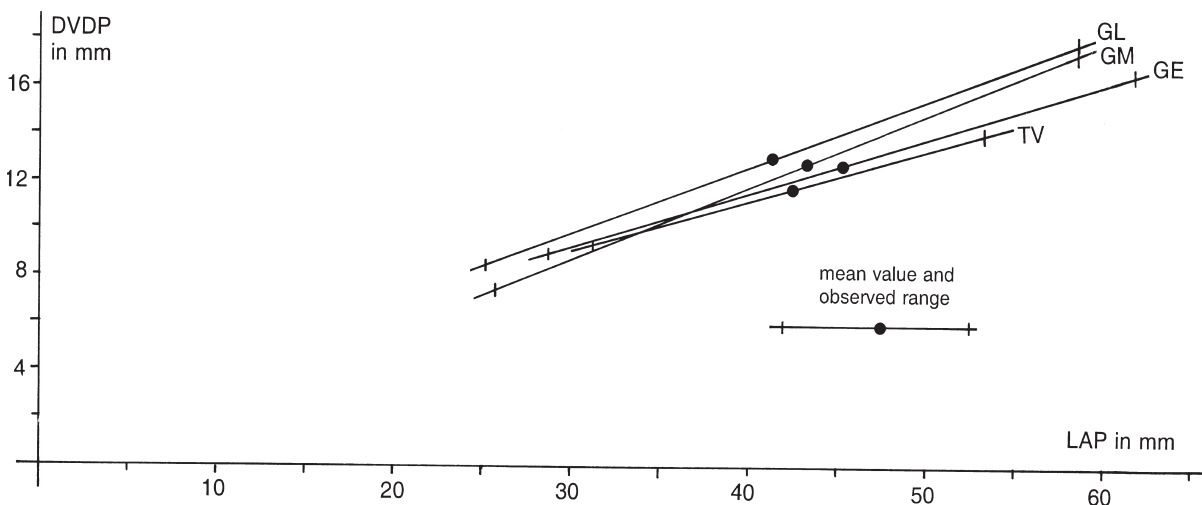


Fig. 11. Four regression lines of the length from the apex to the protoconch (LAP) vs the dorsoventral diameter at the protoconch (DVDP) of *Belemnitella mucronata* (samples GE, GM and GL) and *B. misburgensis* sp. nov. (sample TV). + = mean value. The regression lines of samples GR, TM and TP are very nearly identical to the regression line of sample GM and are not included.

by Christensen (1995). The coefficients of variation of the alveolar angle vary from *c.* 4 to 5 and are thus similar to those shown by Christensen (1995). Thus, it can be concluded that all the samples exhibit an ordinary relative variation.

On the basis of the univariate analyses the samples of *Belemnitella* can be regarded as homogeneous.

Bivariate analysis

The scatter plots and regression lines of the length from the apex to the protoconch vs the dorsoventral diameter at the protoconch of samples GE, GL, GM and TV are shown in Figures 7–10. The scatter plots and regression lines of samples GR, TM and TP are not shown, because these are very closely similar to sample GM.

The equations of the regression lines of samples GE–TV are given in Tables 3–9. The correlation coefficients are very highly significant in all samples ($P < 0.001$, with $N - 2$ degrees of freedom). The y -intercepts were tested by t -tests to see if they differed significantly from zero. The t -tests showed that the y -intercepts did not differ significantly from zero at the 5% level, implying an isometric relationship of the variates. Since the relationship is isometric in all samples it is permissible to calculate the mean values of the Birkelund Index.

The regression lines of samples GE, GL, GM and TV are shown in Figure 11. The regression lines of samples GE and TV were compared with the following result. The variances of the regression lines, slopes and positions did not differ at the 5% level. With regard to the slenderness, therefore, *Belemnitella mucronata* from the uppermost Lower Campanian *gracilis/mucronata* Zone (sample GE) and *B. misburgensis* sp. nov. from the upper part of the '*vulgaris/stolleyi*' Zone (sample TV) cannot be distinguished.

The regression lines of samples GE and GM were compared with the following result. The F -test of the variances of the regression lines shows that these did not differ significantly at the 5% level. The t -test of the slopes showed that these are significantly different ($t_a = 2.0658$; $0.05 > P > 0.025$, with 114 degrees of freedom). The t -test of the positions of the lines gave a value of 2.6717, which is highly significant ($0.01 > P > 0.005$, with 114 degrees of freedom). The specimens of *B. mucronata* from sample GM are thus significantly more stout than the specimens of *B. mucronata* from sample GE.

The regression lines of samples GM and GL were compared with the following result. The F -test of variances of the regression lines showed that these

did not differ significantly at the 5% level. The t -test of the slopes showed that these were not significantly different at the 5% level. The t -test of the positions gave a value of 3.4166, which is very highly significant ($P < 0.001$, with 181 degrees of freedom). The specimens of *B. mucronata* from sample GL are thus significantly more stout than the specimens of *B. mucronata* from sample GM.

On the basis of the bivariate analyses the samples of *Belemnitella* can be regarded as homogeneous, which is consistent with the results obtained from the univariate analyses.

Morphological changes

Based on superficial resemblance alone the nine samples of *Belemnitella* are nearly identical. The guard is stout, usually subcylindrical in ventral view and high conical in lateral view, and slightly flattened ventrally. The apical angle is obtuse or acute and the mucro is distinct in adult specimens, whereas the apical angle is acute and the mucro is only slightly delimited in juvenile specimens. Adult specimens have distinct vascular markings, dorsolateral depressions and dorsolateral double furrows, and both the vascular markings and furrows can be followed to the apex in many specimens. The vascular markings are most conspicuous around the ventral fissure, and in some specimens they may also be relatively distinct on the middle part of the dorsal field. A longitudinal striation is normally developed on the posterior third of the guard. In contrast, juvenile specimens exhibit only a very faint surface texture or no surface texture at all, except for a fine striation posteriorly.

However, on the basis of biometric analyses of the *Belemnitella* lineage, including *B. mucronata* and *B. misburgensis* sp. nov., it has been possible to detect trends in the characters when these are treated quantitatively (Fig. 12).

Length from the apex to the protoconch (LAP)

The maximum LAP in the samples of *B. mucronata* is very closely similar and varies from 56 to 62 mm. The maximum LAP is 53 mm in *B. misburgensis* sp. nov. Following the classification of Christensen (1995) the guard is large in all samples of *B. mucronata* and small in *B. misburgensis* sp. nov. The mean values of the LAP fluctuated, but there seems to be a net decrease in size (Fig. 12).

Some of the means were compared by t -tests with

Table 10. Tabulation of the coefficient of variation for the length from the apex to the protoconch (LAP), Birkelund Index (BI), Schatzky distance (SD), fissure angle (FA) and alveolar angle (AA) for species of *Belemnitella*. After Christensen (1995).

Character	CV
LAP	10–20
BI	10–15
SD	15–25
FA	30–50
AA	4–6

Table 11. Percentage of specimens with a length from the apex to the protoconch larger than 50 mm in *Belemnitella mucronata* from samples GA-TP and *B. misburgensis* sp. nov. from sample TV from the Germania IV and Teutonia I quarries.

Sample	%
TV	3.3
TP	9.3
TM	13.0
GR	13.5
GM	14.1
GL	5.6
GE	15.0
GC	40.9
GA	50.0

Table 12. Percentage of specimens with Birkelund Index less than 3.0 in *Belemnitella mucronata* from samples GA-TP and *B. misburgensis* sp. nov. from sample TV from the Germania IV and Teutonia I quarries.

Sample	%
TV	0
TP	11.6
TM	10.9
GR	10.2
GM	14.1
GL	25.2
GE	0
GC	18.2
GA	0

the following result. The means of samples GC and GE did not differ significantly at the 5% level. The means of samples GE and GL were very highly significantly different ($t_a = 3.5203$; $P < 0.001$, with 146 degrees of freedom). The means of samples GL and GM were significantly different ($t_a = 2.0122$; $0.5 > P > 0.025$, with 184 degrees of freedom). The means of samples TM and TP were also significantly different ($t_a = 2.1598$; $0.5 > P > 0.025$, with 87 degrees of freedom). The means of samples TP and TV did not differ at the 5% level.

The utility of the mean values of the length from the apex to the protoconch is open to discussion, because the proportion of juvenile specimens varies.

However, the trend towards decreasing size seems to be real, because the number of specimens with a LAP larger than 50 mm generally decreases upwards (see Table 11). Sample GL differs from this trend, because the number of specimens with a LAP larger than 50 mm is small and only constitutes c. 6%.

In summary, the LAP shows a zig-zag trend with a net decrease in size, and the number of specimens with a LAP larger than 50 mm generally decreased upwards.

The modes of the histograms are situated in the 40–50 mm size class in all samples (Fig. 6). Thus, it is very likely that the adult stage of both *B. mucronata* and *B. misburgensis* sp. nov. was reached at that size.

Birkelund Index (BI)

Following the classification by Christensen (1995), the guard is stout in all samples, because the mean values of the BI vary from 3.2 to 3.6 (Tables 1–9).

Again, the mean values fluctuated (Fig. 12). The mean value was 3.3 to 3.4 in samples GA and GC, increased to 3.6 in sample GE, decreased to 3.2 in sample GL, increased to 3.4 in samples GM, GR, TM and TP, and increased further to 3.6 in sample TV.

Some of the mean values were compared by *t*-tests with the following result. The means of samples GC and GE were highly significantly different ($t_a = 3.3335$; $0.005 > P > 0.001$, with 60 degrees of freedom). The means of samples GE and GL were very highly significantly different ($t_a = 5.2234$; $P < 0.001$, with 145 degrees of freedom). The means of samples GE and GM were highly significantly different ($t_a = 2.3919$; $0.02 > P > 0.01$, with 116 degrees of freedom). The means of samples GL and GM were highly significantly different ($t_a = 3.1265$; $0.005 > P > 0.001$, with 183 degrees of freedom). The means of samples TP and TV were significantly different ($t_a = 2.5394$; $0.02 > P > 0.01$, with 71 degrees of freedom).

In summary, *B. mucronata* from sample GE is markedly more slender and *B. mucronata* from sample GL is markedly more stout than *B. mucronata* from the other samples. *B. misburgensis* sp. nov. is more slender than *B. mucronata*, except *B. mucronata* from sample GE.

Very stout specimens, with a BI less than 3.0, occurred in all of the samples, except samples GA, GE and TV (Table 12). The absence of very stout specimens in sample GA may be due to the small number of specimens in this sample. The lack of very stout specimens of *B. mucronata* in sample GE and of *B. misburgensis* sp. nov. in sample TV is due to the fact that the mean values of the BI is relatively large ($\bar{X}_{BI} = 3.6$).

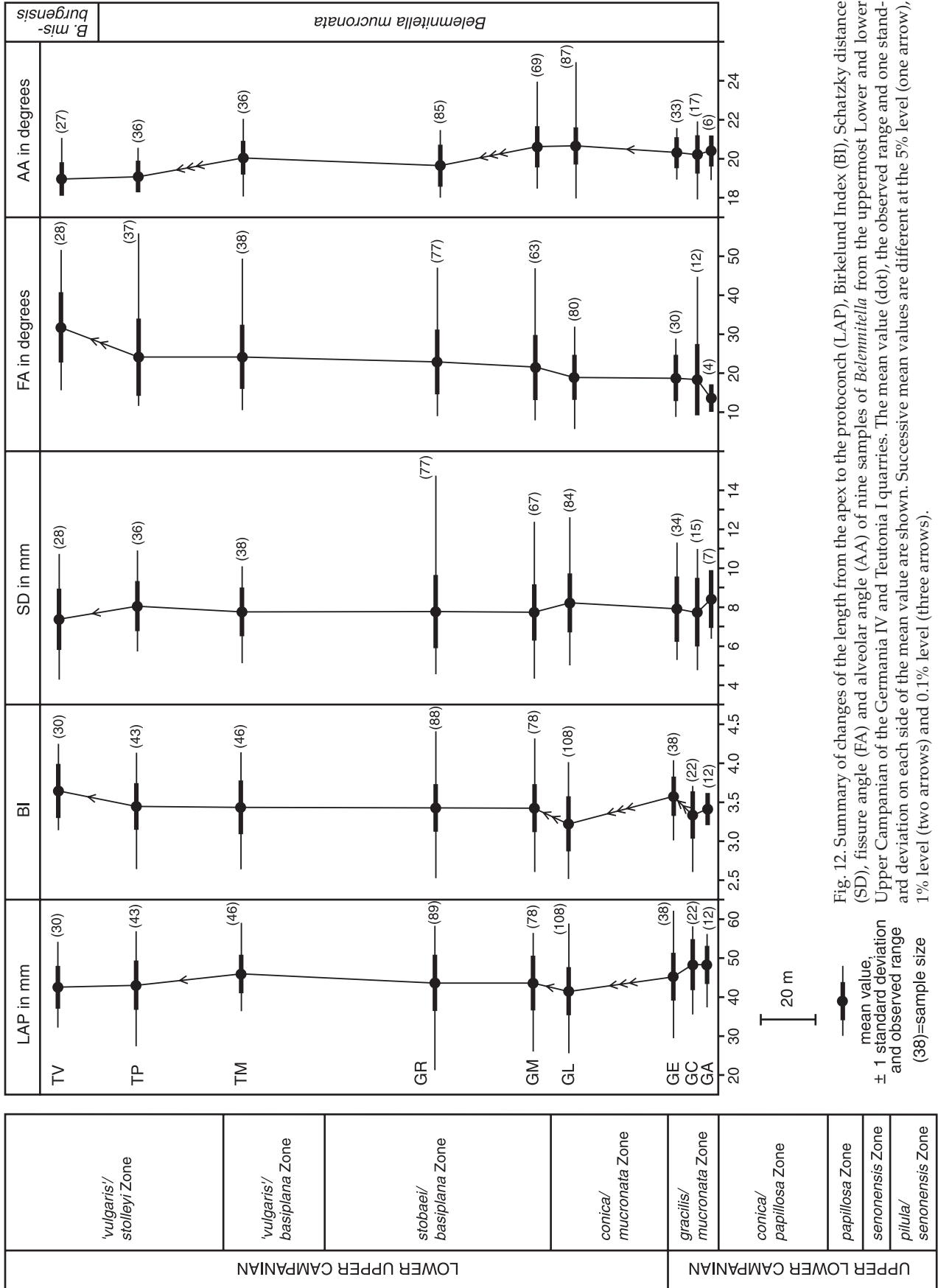


Fig. 12. Summary of changes of the length from the apex to the protoconch (LAP), Birkelund Index (BI), Schatzky distance (SD), fissure angle (FA) and alveolar angle (AA) of nine samples of *Belemnitella* from the uppermost Lower and lower Upper Campanian of the Germania IV and Teutonia I quarries. The mean value (dot), the observed range and one standard deviation on each side of the mean value are shown. Successive mean values are different at the 5% level (one arrow), 1% level (two arrows) and 0.1% level (three arrows).

The large number of very stout specimens of *B. mucronata* in sample GL (c. 25%) is due to the small mean value of the BI ($\bar{X}_{BI} = 3.2$). In general terms the number of very stout specimens decreased stratigraphically upwards (Table 12).

In summary, the slenderness of the guard, as expressed by the mean value of the BI, showed a zig-zag trend in the uppermost Lower and basal Upper Campanian. It was constant in the remaining part of the lower Upper Campanian, except in the uppermost part, where it increases (Fig. 12). Moreover, the number of very stout specimens (BI less than 3) generally decreased upwards.

Stout, strongly vascularized specimens of *Belemnitella* with a truncated apex, from the uppermost Lower and lower Upper Campanian, were previously assigned to *B. mucronata senior* Nowak or *B. senior* Nowak by authors, including Jeletzky (1951) and Schulz (1978). As shown above, very stout specimens occurred in most of the samples of *B. mucronata*. Moreover, the truncation of the apex is a gerontic character and the vascularization became more conspicuous in adult and gerontic specimens of *B. mucronata*. Since *B. senior*-like specimens only constituted a minor component, generally 10–20%, in most of the samples of *B. mucronata*, *B. senior* is here considered merely as an extreme morphological variant of *B. mucronata*.

Schatzky distance (SD)

The SD is medium-sized in all samples. The mean value was c. 8 mm in *B. mucronata* and decreased to c. 7 mm in *B. misburgensis* sp. nov. (Fig. 12). The means of samples TP and TV were compared by the *t*-test, which showed that the means differed significantly ($t_a = 2.0496$; $0.05 > P > 0.025$, with 62 degrees of freedom).

Fissure angle (FA)

The mean values of the FA increased gradually from c. 19° in sample GC to 31° in sample TV (Fig. 12). The mean value of sample GA is only 13.5°, but since it is based upon only four specimens it is unreliable.

The FA is small in *B. mucronata* (mean values are c. 19° to 25°) and medium-sized (mean value c. 30°) in *B. misburgensis* sp. nov. The observed range of the FA is very closely similar in the samples GC and GM-TV, c. 10° to 50°.

Some of the means were compared by *t*-tests with the following result. The means of the samples GA and GE did not differ significantly at the 5% level. The means of the samples GM and GR did not differ

significantly at the 5% level. In contrast, the means of the samples GL and GR differed very highly significantly ($t_a = 3.3805$; $P < 0.001$, with 155 degrees of freedom). The means of samples TP and TV were highly significantly different ($t_a = 3.0679$; $0.005 > P > 0.001$, with 63 degrees of freedom).

Although the means of some of the samples are not statistically different, the trend towards a larger fissure angle seems to be real. The reason that statistically significant differences between successive samples have not been detected is most likely due to the fact that the difference is too small in two closely spaced samples.

Alveolar angle (AA)

The mean values fluctuated and were c. 20° in samples GA, GC and GE, increased to c. 21° in samples GL and GM, decreased to c. 20° in samples GR and TM and decreased further to c. 19° in samples TP and TV (Fig. 12).

Some of the means were compared by *t*-tests with the following results. The means of samples GE and GL were significantly different ($t_a = 2.0599$; $0.05 > P > 0.025$, with 123 degrees of freedom). The means of the samples GM and GR were very highly significantly different ($t_a = 6.0171$; $P < 0.001$, with 152 degrees of freedom), as were the means of the samples TM and TP ($t_a = 4.5112$; $P < 0.001$, with 70 degrees of freedom). The means of the samples GR and TM did not differ significantly at the 5% level.

In summary, the size of the AA angle displayed a zig-zag trend with a net decrease.

Interpretation of the morphological changes

Belemnitella mucronata migrated into northwest Germany in the uppermost Lower Campanian, where it co-occurred with *Goniotentis quadrata gracilis*, the youngest taxon of the genus, in the *gracilis/mucronata* Zone. As shown above, morphological changes have been recognized in the genus *Belemnitella* in the uppermost Lower and lower Upper Campanian of the Lehrte West Syncline. The length from the apex to the protoconch, Birkelund Index and alveolar angle, show reversals with net decreases or increases. The Schatzky distance shows stasis in *B. mucronata* from the uppermost Lower and lower Upper Campanian and decreases in *B. misburgensis* sp. nov. from the uppermost part of the lower Upper Campanian. The fissure an-

SUB-STAGE	BELEMNITE ZONES						RANGE OF SPECIES OF <i>BELEMNITELLA</i> IN VARIOUS AREAS							
	Conventional 1)		Russian Platform 2)		NW Europe 3)		4)		5)		6)		7)	
	UPPER CAMPIANIAN	upper	<i>langei</i>	<i>Belemnitella langei</i>	<i>B. l. najdini</i>	<i>minor</i> II	<i>mucronata</i>	<i>woodi</i>	<i>minor</i> II	<i>mucronata</i>	<i>misburgensis</i> sp. nov.	<i>mucronata</i>	<i>schulzi</i> →	
lower	<i>minor</i>	<i>Belemnitella langei</i>	<i>B. l. langei</i>	<i>minor</i> I	<i>woodi</i>	<i>minor</i> I	<i>minor</i> I	<i>minor</i> I						
		<i>mucronata</i>	<i>Belemnitella mucronata</i>		<i>mucronata</i>									

Fig. 13. Stratigraphical scheme, showing Upper Campanian *Belemnitella* zonation and range of species of *Belemnitella* in various areas. Sources: Column 1, Jeletzky (1951, 1958); column 2, Naidin (1979); column 3, Christensen (1995, 1999, 2000). Column 4 shows the range of species of *Belemnitella* in Norfolk in east England (Christensen 1995), the Mons Basin in south Belgium (Christensen 1999) and the Maastricht-Liège district in The Netherlands and Belgium (Keutgen 1995, Keutgen & Jagt 1999). Column 5 shows the lower Upper Campanian belemnite succession of Misburg-Höver (this paper). The upper Upper Campanian belemnites of this area are poorly known and are, therefore, not included. Column 6 shows the range of *B. mucronata* in the Kristianstad and Båstad Basins, in addition to the Vomb Trough, in Scania (Christensen 1975, 1986, 1993). Upper Upper Campanian rocks have not been recognized there. Column 7 shows the range of *B. schulzi* in the chalk pit at Krons Moor in northwest Germany (Christensen 2000). The belemnites from the lower and middle part of the Upper Campanian of Krons Moor need revision and are, therefore, not included.

gle displays unidirectional change and increases gradually. These morphological changes are interpreted as long-term phyletic gradualism.

The samples of *Belemnitella* were collected from an expanded succession consisting of monotonous calcareous marls and marly limestones, which does not show any sign of interruptions and non-sequences, and the samples can be regarded as homogeneous on the basis of the biometric analyses (see above). Thus, the present study meets the requirements for the analysis of morphological variation within a fossil lineage as suggested by Smith & Paul (1985).

Sheldon (1987, 1990a, 1990b, 1993, 1996) has discussed two models of evolution, the well-known phyletic gradualism model and the punctuated equilibrium model of Eldredge & Gould (1972), in addition to the influence of the environment upon these models. The phyletic gradualism model has almost universally been depicted as unidirectional change, but Sheldon argued that it is to be expected to find reversals in any character of a lineage that maintains a range of variation, because of fluctuating selection pressure. This is the so-called 'zig-zag evolution' of Henningsmoen (1964). Sheldon (1993: 22) even argued '... that if one has not found reversals, the lineage has not been sampled in sufficient detail.'

The morphological changes seen in the *Belemnitella* lineage could be explained either as ecophenotypic variation or related to multiple extinctions and succeeding immigrations from elsewhere. It seems that ecophenotypic variation can be ruled out since the uppermost Lower and lower Upper Campanian monotonous sediments of the Lehrte West Syncline were deposited in a fairly stable environment. The hypothesis of multiple extinctions and succeeding immigrations can likewise be excluded, because the lower Upper Campanian *Belemnitella* succession of the Lehrte West Syncline differs in part from those of Scania in southern Sweden (Christensen 1975, 1986, 1993), Norfolk in eastern England (Christensen 1995), the Mons Basin in southern Belgium (Christensen 1999) and the Maastricht-Liège district in The Netherlands and Belgium (Keutgen 1995, Keutgen & Jagt 1999) (Fig. 13). In Norfolk, the Maastricht-Liège district and the Mons Basin, *B. mucronata* occurred in the lower part of the lower Upper Campanian and *B. woodi* occurred in the upper part of the lower Upper Campanian. In Scania, *B. mucronata* ranged throughout the entire lower Upper Campanian.

In contrast, it seems that local populations of *Belemnitella* from slightly different habitats evolved in different directions. The samples of *Belemnitella* from

Scania were collected in near-shore sediments, whereas the samples from Norfolk, the Maastricht-Liège district and the Mons Basin came from offshore chalks. The sediments of the Lehrte West Syncline were deposited at depths less than that of the chalk. In this context, it is noteworthy that the evolutionary development of populations of the Middle Coniacian-Lower Campanian *Goniatoteuthis* lineage was delayed in some areas (Christensen 1997a). For instance, coeval populations of the middle Lower Campanian *Goniatoteuthis q. quadrata* from the chalks of Lägerdorf and marls of Misburg-Höver differed with respect to the depth of the pseudoalveolus; the specimens from Misburg-Höver had a slightly deeper pseudoalveolus. The specimens from Lägerdorf were thus phylogenetically retrograde compared to the coeval specimens from Misburg-Höver. The uppermost Lower Campanian *G. quadrata scaniensis* Christensen, 1975 from Scania was also phylogenetically retrograde in comparison with the coeval *G. quadrata gracilis* from northwest Germany. Populations of *Goniatoteuthis* from the Late Santonian of Yorkshire were phylogenetically retrograde in comparison with coeval populations from northwest Germany (Ernst 1966, Mitchell 1994, 1995).

The Plus ça change model of Sheldon (1990b, 1996) predicts continuous phyletic evolution in narrowly-fluctuating, slowly changing environments, whereas stasis tends to prevail in widely-fluctuating environments, over geological time-scales. The evolution of the uppermost Lower and lower Upper Campanian *Belemnitella* lineage in the Lehrte West Syncline is thus consistent with the former model.

The Upper Campanian *Belemnitella* zonation of Europe

Christensen (1999) reviewed the Upper Campanian *Belemnitella* zonations of northwest Europe. The conventional zonation comprises three interval zones, the *B. mucronata*, *B. minor* and *B. langei* Zones, and was introduced by Jeletzky (1951) (Fig. 13). It has been used subsequently by numerous workers, but it was critically assessed by Christensen (1995, 1996, 1999), who argued that the *B. minor* and *B. langei* Zones of Jeletzky should not be maintained. A slightly different zonation is used on the Russian Platform (Fig. 13). Two zones are recognized, the *B. mucronata* Zone below and the *B. langei* Zone above (Naidin 1979). The latter is subdivided into three subzones, the *B. langei minor*, *B. l. langei* and *B. langei najdini* Subzones. Chri-

stensen (1995, 1996, 1999, 2000) argued, however, that *B. minor* should neither be considered as a subspecies of *B. langei*, as suggested by Naidin (1979), nor placed in the *B. langei* group, as assigned by Kongiel (1962), because it differs markedly from this species. Christensen (1995, 1996, 2000) considered *B. najdini* to be a legitimate species, which belonged to the *B. langei* group.

Christensen (1999) showed that the subdivision of the Upper Campanian chalks of Norfolk, England into four informal *Belemnitella* zones on the basis of large to very large species (Christensen 1995) could be applied to the Maastricht-Liège district in The Netherlands and Belgium (Keutgen 1995, Keutgen & Jagt 1999), the Mons Basin in Belgium (Christensen 1999), and the Misburg-Höver-Ahlten area in Germany (Christensen 1995, Niebuhr et al. 1997, Ernst et al. 1997b). These zones are, in ascending order, the lower Upper Campanian *B. mucronata* Zone below and *B. woodi* Zone above, and the upper Upper Campanian *B. minor* I Zone below and *B. minor* II Zone above (Fig. 13). Christensen (1999) suggested, therefore, that these zones might be regarded as formal zones, because they had been recognized in widely-spaced areas in northwest Europe.

However, in the Misburg-Höver area, the zonal scheme that was apparently applicable from eastern England to Germany cannot be applied. Here *B. woodi* has not yet been found, and *B. mucronata* ranged throughout the lower Upper Campanian except the highest part (upper '*vulgaris/stolleyi* Zone), where it was replaced by *B. misburgensis* sp. nov. (Fig. 12). The last species is known to range up to c. 12 m below the top of the lower Upper Campanian. The belemnites from this highest interval, and from the lower part of the upper Upper Campanian as determined by Niebuhr et al. (1997, Fig. 2), have not been investigated. In Scania *B. mucronata* ranged throughout the lower Upper Campanian (Christensen 1975, 1986, 1993) (Fig. 13). Moreover, *B. minor* II did not occur in the upper part of the upper Upper Campanian of Krons Moor; it was replaced there by *B. schulzi* Christensen (Christensen 2000) (Fig. 13). The species of *Belemnitella* from the lower and middle Upper Campanian of Krons Moor need revision.

It can thus be concluded that the Upper Campanian *Belemnitella* successions of Norfolk, the Maastricht-Liège district and the Mons Basin, which are identical, differ in part from those of the Misburg-Höver-Ahlten area, Krons Moor and Scania. Consequently, the suggestion by Christensen (1999) that the *Belemnitella* zonations of Norfolk, the Mons Basin and the Maastricht-Liège district can be used as formal zones throughout northwest Europe is perhaps no longer tenable.

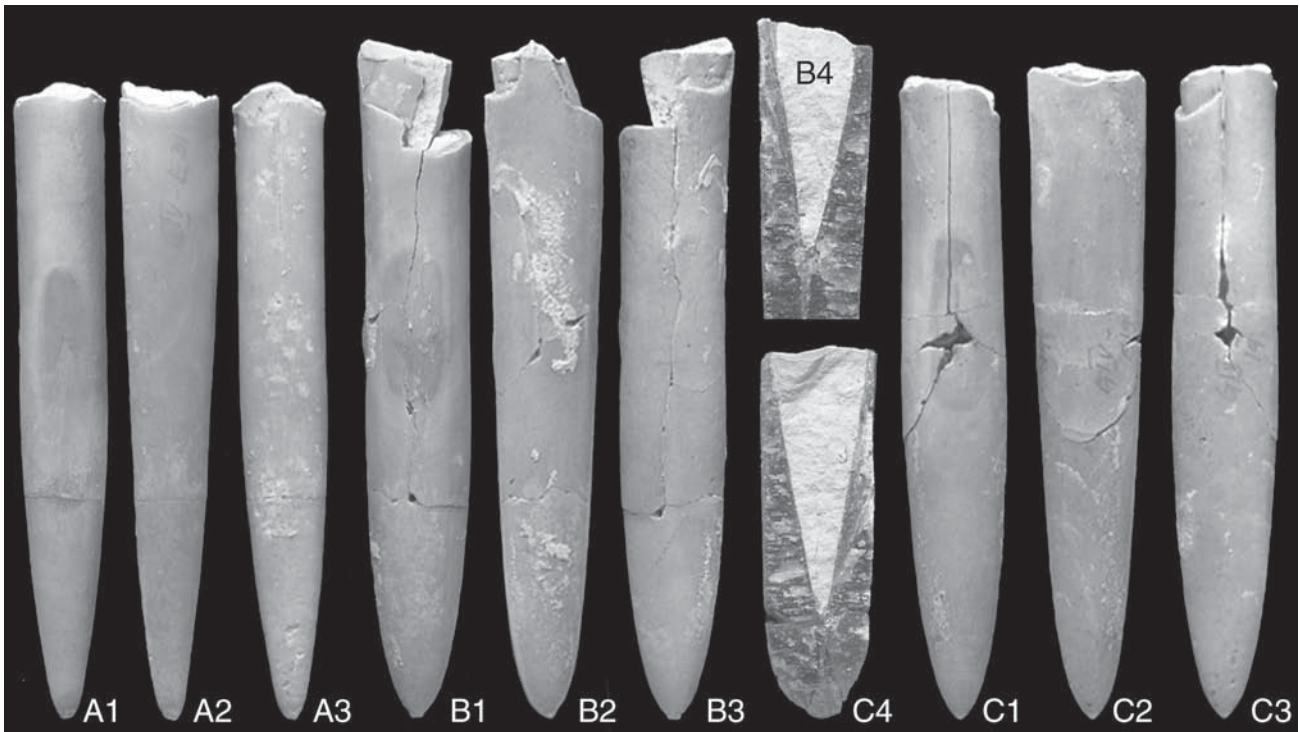


Fig. 14. *Belemnitella praecursor*, uppermost Lower Campanian, upper part of the *gracilis/mucronata* Zone, Germania IV quarry. Specimens are coated with ammonium chloride, except Figs B4 and C4, and are natural size.

A. MGUH 25724, medium-sized, slender specimen with a smooth guard and tapering apical end. 1, dorsal view; 2, lateral view; 3, ventral view. B. MGUH 25725, medium-sized specimen with an almost smooth guard. 1, dorsal view; 2, lateral view; 3, ventral view; 4, view of the split anterior, end showing internal characters. Schatzky distance, 8.6 mm; fissure angle, 11.0°; alveolar angle, 21.0°; Birkelund Index, 3.4. C. MGUH 25726, medium-sized specimen with an almost smooth guard. 1, dorsal view; 2, lateral view; 3, ventral view; 4, view of the split anterior end, showing internal characters. Schatzky distance, 7.0 mm; fissure angle, 18.0°; alveolar angle, 20.0°; Birkelund Index, 3.6.

Systematic Palaeontology

Family Belemnitellidae Pavlow, 1914
[ICZN 1985; Opinion 1328; name no. 572]

Diagnosis. – See Christensen (1997a).

Distribution. – Belemnitellids occurred only in the Northern Hemisphere and have been recorded from the North European and North American Provinces, in addition to the northern margin of the Tethyan Realm in Europe (Christensen 1997a, 1997b). They occurred only in the Upper Cretaceous and became extinct at the Maastrichtian-Danian boundary.

Genus *Belemnitella* d'Orbigny, 1840
[ICZN 1985; Opinion 1328; name no. 2269]

Type species. – *Belemnites mucronatus* Schlotheim, 1813, by subsequent designation of Herrmannsen (1846); ICZN Opinion 1328 (1985), name no. 2979.

Diagnosis. – See Christensen (1997a).

Distribution. – *Belemnitella* was widely distributed and occurred in the North European and North American Provinces, in addition to the northern part of the Tethyan Realm in Europe. Christensen (1997a) noted that it appeared at the base of the Santonian and continued to the top of the Maastrichtian. However, at the Symposium on Cretaceous Stage Boundaries in Brussels 1995, it was proposed that the base of the Santonian should be placed at the lowest occurrence of *Inoceramus (Cladoceramus) undulatopectatus* (Roemer) (Lamolda & Hancock 1996). Following this definition, the earliest species of *Belemnitella*, *B. schmidi* Christensen & Schulz, 1997 is of latest Coniacian age. *Belemnitella* was a very long-ranging species, about 21 million years longevity (Christensen 1997a).

Belemnitella praecursor Stolley, 1897
Fig. 14

Synonymy. – See Christensen & Schmid (1987).

Holotype. – By monotypy, the original of Stolley (1897, Pl. 3, fig. 24). It came from the basal Lower Campanian *Goniatites granulataquadrata* Zone, Broitzem pit, Braunschweig, and is housed in the Geologisch-Paläontologisches Institut, Kiel, Germany. A cast of the type was figured by Christensen (1986, Pl. 3, fig. 4) and by Christensen & Schmid (1987, Pl. 3, figs 4–5).

Material. – Three specimens, MGUH 25724–25726, from the upper part of the uppermost Lower Campanian *gracilis/mucronata* Zone of the Germania IV quarry at Misburg, that is between beds KM 24 and KM 25, 0 to 5.3 m below the boundary between the Lower and Upper Campanian.

Dimensions. – Measurements of the critical characters of MGUH 25725–25726 are shown in Table 13.

Description. – MGUH 25724 (Fig. 14A) is an adolescent specimen, which has a smooth and slender guard with an acute apical end without a mucro. It is slightly lanceolate in ventral view, high conical in lateral view and flattened ventrally. The internal characters are unknown, because the guard cannot be split in the median plane.

MGUH 25726 (Fig. 14C) has an almost smooth, ventrally flattened guard, which is slightly lanceolate in ventral view and high conical in lateral view. The apical end is acute without a mucro. The Schatzky distance is medium-sized, the fissure angle is small, the alveolar angle is large, and the bottom of the ventral fissure is straight with an outward bend.

MGUH 25725 (Fig. 14B) has slightly developed vascular markings, dorsolateral depressions and double furrows and the apical end is acute with a poorly delimited mucro. The guard is subcylindrical in ventral view, high conical in lateral view and flattened ventrally. The Schatzky distance is medium-sized, the fissure angle is small, the alveolar angle is large, and the bottom of the ventral fissure is straight with an outward bend.

Discussion. – *B. praecursor* was established on the basis of only one adult specimen and characterized by

its smooth guard (Stolley 1897). Later, Jeletzky (1955) emended the diagnosis and included specimens with vascular markings and longitudinal striae in this species. Moreover, he distinguished three varieties: var. *praecursor*, which has a smooth guard; var. *mucronatiformis* Jeletzky, 1955, which has vascular markings and longitudinal striae; and var. *media* Jeletzky, 1955, which is morphologically intermediate between var. *praecursor* and var. *mucronatiformis*.

Christensen & Schmid (1987) studied the variation of critical characters in a large sample of *B. praecursor* from the lower Lower Campanian *lingua/quadrata* Zone of the CPL quarry at Hallembaye in Belgium. Christensen (1991) analyzed biometrically a sample from the middle Lower Campanian, top *pilula*-basal *quadrata* Zone *sensu anglico*, from East Harnham in Wiltshire, southern England. Christensen & Schmid (1987) and Christensen (1991) did not distinguish subspecies of *B. praecursor*, but noted that extreme variants with a smooth guard occurred at East Harnham (Christensen 1991, Pl. 5, figs 3–4), but not at Hallembaye.

MGUH 25724–25725 are assigned to *B. praecursor*, because they have a smooth or almost smooth guard with an acute apical end. They differ in no significant respect in their internal characters from *B. praecursor*.

MGUH 25724 (Fig. 14A) is very closely similar with respect its size, slenderness, shape, smooth guard and acute apical end without a mucro to a specimen of *B. praecursor* from the lower Lower Campanian *lingua/quadrata* Zone of Lägerdorf (Ernst 1964, Pl. 1, fig. 1).

Distribution. – *B. praecursor* has been recorded from Northern Ireland, through England, France, Belgium, northern Germany and Poland to Russia (Christensen 1991). It has been reported from the Upper Santonian and lower and middle Lower Campanian. It was assumed previously that *B. praecursor* was replaced by *B. mucronata* in the uppermost Lower Campanian. However, the record of *B. praecursor* from the Germania IV quarry, 0 to 5.3 m below the boundary between the Lower and Upper Campanian, shows that this species ranged to or almost to the top of the Lower Campanian.

Table 13. Measurements of critical characters of *Belemnitella praecursor*, upper part of the *gracilis/mucronata* Zone, Germania IV quarry.

Specimen	LAP	DVDP	LDP	MLD	SD	FA	AA	BI
MGUH 25726	50.7	13.9	14.1	14.1	7.0	18.0	20.0	3.6
MGUH 25725	46.5	13.7	13.9	13.9	8.6	11.0	21.0	3.4

Belemnitella mucronata (Schlotheim, 1813)
Plate 1, figs 1–18; Plate 2, figs 1–8

Synonymy. – See Christensen (1995).

Neotype. – Specimen no. kca 5/2 in the Collections of the Niedersächsisches Landesamt für Bodenforschung, Hannover. It came from the middle part of the lower Upper Campanian *stobaei/basiplana* Zone of the Germania IV quarry at Misburg near Hannover (Christensen et al. 1975, Pl. 1, fig. 1).

Material. – 375 specimens, including MGUH 25727–25732, from the uppermost Lower Campanian *gracilis/mucronata* Zone and lower Upper Campanian *conica/mucronata* and *stobaei/basiplana* Zones of the Germania IV quarry. 232 specimens, including MGUH 25733–25735, from the lower Upper Campanian '*vulgaris*'/*basiplana* Zone and middle part of the '*vulgaris*'/*stolleyi* Zone of the Teutonia I quarry.

Description. – Guard large and stout; generally subcylindrical in ventral view and high conical to subcylindrical in lateral view; guard flattened over its entire length; apical end acute or obtuse with a well defined mucro; mean value of the Birkelund Index usually 3.3 to 3.6; Schatzky distance medium-sized to large (mean values 7 to 9.5 mm); fissure angle small (mean values 15 to 25°); alveolar angle large (mean values generally 20 to 21°); bottom of ventral fissure commonly straight; adult specimens with distinct vascular markings and dorso-lateral depressions that continue posteriorly in dorso-lateral double furrows; longitudinal striae usually present, less distinct than vascular markings.

Discussion. – Samples GA-TP from the uppermost Lower Campanian and lower Upper Campanian are assigned to *B. mucronata*, because the specimens in these samples differ in no significant respect from this species.

As shown above, *B. mucronata* from sample GE differs from the other samples of this species in its more slender guard and lack of very stout specimens. *B. mucronata* from sample GL differs from the other samples of this species in its slightly smaller size of the guard, smaller number of specimens with a length from the apex to the protoconch larger than 50 mm, and larger number of very stout specimens.

In spite of these differences, these two samples are placed in *B. mucronata* because they fall within the variation of this species. For example, Christensen (1995, Table 2) recorded samples of *B. mucronata* from the uppermost Lower and lower Upper Campanian of Scania with mean Birkelund Indices of 3.6–3.7, and

Christensen (1999, Table 1) described a sample of *B. mucronata* from the basal Upper Campanian of the Mons Basin, which had a mean Birkelund Index of 3.3.

B. mucronata differs from the lower and middle Lower Campanian *B. alpha* Naidin in its smaller guard, smaller Schatzky distance, larger fissure angle, conspicuous vascular markings and well-defined mucro; and from the Upper Santonian-Lower Campanian *B. praecursor* in its smaller and more stout guard, larger fissure angle, strongly developed vascular markings and well defined mucro. *B. mucronata* is closely similar to *B. woodi* Christensen from the upper part of the lower Upper Campanian, but differs in its larger Schatzky distance, larger fissure angle, smaller alveolar angle, and more weakly developed vascular markings. *B. mucronata* is also closely similar to *B. minor* I Jeletzky and *B. minor* II Christensen, but differs from these subspecies in its smaller guard, smaller Schatzky distance, smaller fissure angle and larger alveolar angle. Moreover, *B. mucronata* is more stout than *B. minor* I. The affinity to *B. misburgensis* sp. nov. is discussed below.

Distribution. – *B. mucronata* was widespread in the North European Province and possibly also occurred in the northern European part of the Tethyan Realm. It appeared in the uppermost Lower Campanian, *gracilis/mucronata* Zone, and continued into the lower Upper Campanian. Records from the upper Upper Campanian and Lower Maastrichtian are misconceptions (Christensen 1998).

Belemnitella misburgensis sp. nov.
Plate 2, figs 9–22

Holotype. – MGUH 25736 from the upper part of the '*vulgaris*'/*stolleyi* Zone, uppermost lower Upper Campanian, Teutonia I quarry at Misburg near Hannover, north Germany (Pl. 2, figs 9–12).

Dimensions of the holotype. – Length from apex to protoconch, 53.4 mm; dorsoventral diameter at protoconch, 14.4 mm; lateral diameter at protoconch, 15.4 mm; maximum lateral diameter, 15.4 mm; Schatzky distance, 9.0 mm; fissure angle, 39.0°; alveolar angle, 18.0°; Birkelund Index, 3.7.

Material. – 100 specimens, including MGUH 25736–25739, from the upper part of the '*vulgaris*'/*stolleyi* Zone, immediately above bed M 133 to bed KM 140, uppermost lower Upper Campanian, Teutonia I quarry, Misburg.

Diagnosis. – Guard small and stout; Schatzky distance medium-sized; fissure angle medium-sized; alveolar angle small; conspicuous vascular markings; and well defined mucro.

Description. – Guard small (maximum length from apex to protoconch less than 55 mm) and stout; sub-cylindrical in ventral view and subcylindrical or high conical in lateral view; guard flattened over its entire length; dorsoventral diameter at protoconch generally smaller than lateral diameter at protoconch; relationship between length from apex to protoconch and dorsoventral diameter at protoconch isometric; mean value of Birkelund Index 3.6, with an observed range from 3.1 to 4.4 mm; apical end acute or obtuse, with well-defined mucro.

Schatzky distance medium-sized, mean value *c.* 7 mm, with an observed range from *c.* 4 to 11 mm; fissure angle medium-sized, mean value *c.* 31°, with an observed range from *c.* 15 to 51°; alveolar angle small, mean value *c.* 19°, with an observed range from 18 to 21°.

Dorso-lateral depressions and double furrows fully developed; vascular markings conspicuous.

Biometry. – The results of the univariate and bivariate biometric analyses of sample TV, from the upper part of the 'vulgaris'/stolleyi Zone, are shown in Table 9. The correlation coefficient is very highly significant ($P < 0.001$, with 28 degrees of freedom). The *t*-test on the *y*-intercept gave a value of 1.7803, which is not significant ($0.10 > P > 0.05$, with 28 degrees of freedom), implying an isometric relationship of the variates.

Discussion. – *B. misburgensis* sp. nov. is closely similar to *B. mucronata*, its ancestor, with respect to shape and surface markings, but differs in its slightly smaller and more slender guard, in addition to its smaller Schatzky distance and larger fissure angle. Moreover, the alveolar angle of *B. misburgensis* sp. nov. is smaller than in the samples of *B. mucronata*, except sample TP, the highest level of occurrence of the species in the Misburg-Höver area.

B. misburgensis sp. nov. is also closely similar to the coeval *B. woodi* Christensen, which was first described from Norfolk, England (Christensen 1995), and later recorded from northeast Belgium (Keutgen 1995, Keutgen & Jagt 1999) and the Mons Basin in southern Belgium (Christensen 1999).

B. woodi has a large and stout guard, a large Schatzky distance (the weighted grand mean of five samples from Norfolk is 9.5 mm), a medium-sized fissure angle (means from 25° to 30°) and a small alveolar

angle (mean *c.* 19°). The vascular markings are well developed around the ventral fissure and weakly developed or not present elsewhere (Christensen 1995). Two stratigraphically forms have been recognized; the mean Birkelund Index is 3.3–3.4 in the early form and 3.7–3.8 in the late form (Christensen 1995).

The mean value of the Schatzky distance of *B. misburgensis* sp. nov. was compared by *t*-tests with the mean values of the Schatzky distance of the early form of *B. woodi* from Weybourne (mean value 10.6 mm) and the late form of *B. woodi* from Catton Grove (mean value 8.7 mm) in Norfolk (see Christensen 1995). The means of the samples of *B. misburgensis* sp. nov. and the early form of *B. woodi* were very highly significantly different ($t_a = 5.5738$; $P < 0.001$, with 50 degrees of freedom). The means of the samples of *B. misburgensis* sp. nov. and the late form of *B. woodi* were significantly different ($t_a = 2.6324$; $0.02 > P > 0.01$, with 35 degrees of freedom).

B. misburgensis sp. nov. differs from the early and late forms of *B. woodi* in its slightly smaller guard, smaller Schatzky distance and more conspicuous vascular markings. Moreover, it differs from the early form of *B. woodi* in its more slender guard.

Distribution. – For the time being, *B. misburgensis* sp. nov. has been recorded only from the uppermost part of the lower Upper Campanian, upper part of the 'vulgaris'/stolleyi Zone, of the Teutonia I quarry at Misburg.

Acknowledgements

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Plate 1

Belemnitella mucronata, uppermost Lower and lower Upper Campanian, Germania IV quarry. Specimens are coated with ammonium chloride, except Figs 4, 6, 8, 10, 14 and 18, and are natural size. Figs 1–8, uppermost Lower Campanian, upper part of the *gracilis/mucronata* Zone, from sample GE. Figs 9–18, lower part of lower Upper Campanian, upper part of the *conica/mucronata* Zone, from sample GL.

Figs 1–4. MGUH 25727, large specimen with an average shape. 1, dorsal view; 2, lateral view; 3, ventral view; 4, view of the split anterior end, showing internal characters. Schatzky distance, 7.5 mm; fissure angle, 26.0°; alveolar angle, 21.0°; Birkelund Index, 3.4.

Figs 5–6. MGUH 25728, large specimen with a slender guard. 5, ventral view; 6, view of the split anterior end, showing internal characters. Schatzky distance, 8.8 mm; fissure angle, 24.0°; alveolar angle, 20.0°; Birkelund Index, 3.9.

Figs 7–8. MGUH 25729, a medium-sized specimen with a slender guard. 7, ventral view; 8, view of the split anterior end, showing internal characters. Schatzky distance, 5.3 mm; fissure angle, 25.5°; alveolar angle, 20.0°; Birkelund Index, 4.1.

Figs 9–10. MGUH 25730, large specimen with a stout guard. 9, ventral view; 10, view of the split anterior end, showing internal characters. Schatzky distance, 9.4 mm; fissure angle, 18.0°; alveolar angle, 21.0°; Birkelund Index 2.9.

Figs 11–14. MGUH 25731, large specimen with an average shape. 11, dorsal view; 12, lateral view; 13, ventral view; 14, view of the split anterior end, showing internal characters. Schatzky distance, 8.7 mm; fissure angle, 18.5°; alveolar angle, 20.0°; Birkelund Index, 3.5.

Figs 15–18. MGUH 25732, large specimen with a very stout guard. 15, dorsal view; 16, lateral view; 17, ventral view; 18, view of the split anterior end, showing internal characters. Schatzky distance, 8.0 mm; fissure angle, 19.5°; alveolar angle, 20.5°; Birkelund Index, 2.5.



Plate 2

Belemnitella mucronata and *B. misburgensis* sp. nov. from the Teutonia I quarry. Specimens are coated with ammonium chloride, except Figs 2, 4, 8, 12, 14, 18 and 22, and are natural size. Figs 1–8. *B. mucronata*, upper part of the lower Upper Campanian, middle part of the 'vulgaris'/stolleyi Zone, from sample TP. Figs 9–22. *B. misburgensis* sp. nov., upper part of the lower Upper Campanian, upper part of the 'vulgaris'/stolleyi Zone, from sample TV.

Figs 1–2. MGUH 25733, large specimen with an average shape. 1, ventral view; 2, view of the split anterior end, showing internal characters. Schatzky distance, 7.9 mm; fissure angle, 16.0°; alveolar angle, 19.0°; Birkelund Index, 3.4.

Figs 3–4. MGUH 25734, medium-sized specimens with an average shape. 3, ventral view; 4, view of the split anterior end, showing internal characters. Schatzky distance, 5.8 mm; fissure angle, 33.0°; alveolar angle, 19.5°; Birkelund Index, 3.7.

Figs 5–8. MGUH 24735, large specimen with a very stout guard, which is slightly lanceolate in ventral view. 5, dorsal view; 6, lateral view; 7, ventral view; 8, view of the split anterior end, showing internal characters. Schatzky distance, 9.4 mm; fissure angle, 11.5°; alveolar angle, 19.0°; Birkelund Index, 2.6.

Figs 9–12. MGUH 25736, holotype, largest specimen with an average shape. 9, dorsal view; 10, lateral view; 11, ventral view; 12, view of the split anterior end, showing internal characters. Schatzky distance, 9.0 mm; fissure angle, 39.0°; alveolar angle, 18.0°; Birkelund Index, 3.7.

Figs 13–14. MGUH 25737, paratype, medium-sized specimen with an average shape. 13, ventral view; 14, view of the split anterior end, showing internal characters. Schatzky distance, 7.4 mm; fissure angle, 30.0°; alveolar angle, 18.0°; Birkelund Index, 3.6.

Figs 15–18. MGUH 25738, paratype, medium-sized specimen with a stout guard, which is slightly lanceolate in ventral view. 15, dorsal view; 16, lateral view; 17, ventral view; 18, view of the split anterior end, showing internal characters. Schatzky distance, 6.8 mm; fissure angle, 24.5°; alveolar angle, 19.0°; Birkelund Index, 3.2.

Figs 19–22. MGUH 25739, paratype, medium-sized specimen with a slender guard, which is slightly lanceolate in ventral view. 19, dorsal view; 20, lateral view; 21, ventral view; 22, view of the split anterior end, showing internal characters. Schatzky distance, 6.0; fissure angle, 25.0°; alveolar angle, 18.0°; Birkelund Index, 4.3.

