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The Belemnites of the Vaals Formation from the C.P.L. Quarry at Hallembaye/Belgium – Taxonomy, Biometry and Biostratigraphy –

With 9 figures and 3 plates

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Die Belemniten-Faunen des unteren bis mittleren Unter-Campan von NW-Europa werden diskutiert. Die Belemniten-Vergesellschaftung der Vaals-Formation ist ungewöhnlich, da sie nur aus zwei Arten besteht: *G.q. quadrata* und *B. praecursor*. Letztere ist hier häufiger als irgendwo in Europa.

[белемниты формации Vaals из каменного карьера C.P.L. (Ciment Portland Liégeoise) близ Halembaye в Бельгии: таксономия, биометрия и биостратиграфия].

Реюме: Было изучено при помощи биометрических методов большое число *Belemnitella praecursor* STOLLEY из формации Vaals каменного карьера C.P.L. близ Hallembaye в Бельгии с целью анализа вариации. Этот вид в близком родстве с *B. alpha* NAIDIN и *B. mucronata* (SCHLOTHEIM); обсуждены отношения.

B. praecursor встречается вместе с *Gonioteuthis quadrata quadrata* (BLAINVILLE), который также исследуется биометрическими методами. Материал *G.q. quadrata* из Hallembaye сопоставляется с материалом *Gonioteuthis* хорошо известных стратиграфических горизонтов. Из этого следует, что формация Vaals каменного карьера C.P.L. относится к низу нижнего кампана, являющегося равным нижней части зоны *lingua/quadrata* sensu germanico.

Обсуждены белемнитовые фауны нижней до средней частей нижнего кампана Северо-Западной Европы. Белемнитовая ассоциация формации Vaals необыкновенна, так как она состоит только из двух видов: *G.q. quadrata* и *B. praecursor*. Последний встречается здесь чаще, чем где-нибудь в другом месте в Европе.

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1. Introduction

The genus *Belemnitella* D'ORBIGNY is usually rare in the lower to middle Lower Campanian of NW Europe. CHRISTENSEN (1986) tentatively recognized two taxa of *Belemnitella* from the lower and middle part of the Lower Campanian: *B. praecursor* STOLLEY and *B. alpha* NAIDIN, and they were fully discussed. JELETZKY (1955a) discussed the concept of *B. praecursor* and distinguished three varieties of *B. praecursor*, but failed to present appropriate biometric analysis of the varieties.

B. praecursor occurs frequently in the Vaals Formation (earlier referred to as "Smectite") in the C.P.L. quarry at Hallembaye in Belgium, as does *Gonioteuthis quadrata quadrata* (BLAINVILLE). A large sample of *B. praecursor* was therefore subjected to biometric analysis in order to study the variation of critical characters. The sample of *G.q. quadrata* was compared to other samples of *Gonioteuthis* in order to place the Vaals Formation of the C.P.L. quarry within the international stratigraphic framework.

2. Previous Work

The first detailed biostratigraphic zonation of the Campanian-Maastrichtian of the Limburg area in Belgium and the Netherlands was presented by SCHMID (1959, 1967). Later on, the lithology, lithostratigraphy, and biostratigraphy of the Upper Cretaceous of that area were studied by FELDER (1975), ALBERS (1976), ALBERS & FELDER (1979), VAN DER TUUK & BOR (1980), FELDER, FELDER & BROMLEY (1980), JAGT (1984), and ROBASZYNSKI et al. (1985), who also gave a historical review of the subdivision of the Campanian-Maastrichtian.

3. Locality

The C.P.L. quarry (Ciment Portland Liegeoise) is situated on the left bank of the Meuse (Maas) River near Hallembaye, about 10 km south of Maastricht (Fig. 1), and exposes the Vaals Formation below and the Gulpen Formation above (Fig. 2).

The Vaals Formation, which has a maximum thickness of about 150 m, is only about 20 m thick around Hallembaye (ROBASZYNSKI et al. 1985) and consists of glauconitic silt with clayey and marly beds. The lower part of the Vaals Formation is exposed in the C.P.L. quarry (ROBASZYNSKI et al. 1985: 5). The sediments of the Vaals Formation were laid down in a near-shore shallow water environment close to the Ardenno-Rhenish Massif (ALBERS 1976, ALBERS & FELDER 1979, ROBASZYNSKI et al. 1985).

Belemnites occur commonly in the upper 2–3 m of the Vaals Formation in the C.P.L. quarry, and the majority of the belemnites studied were collected in situ by the authors.

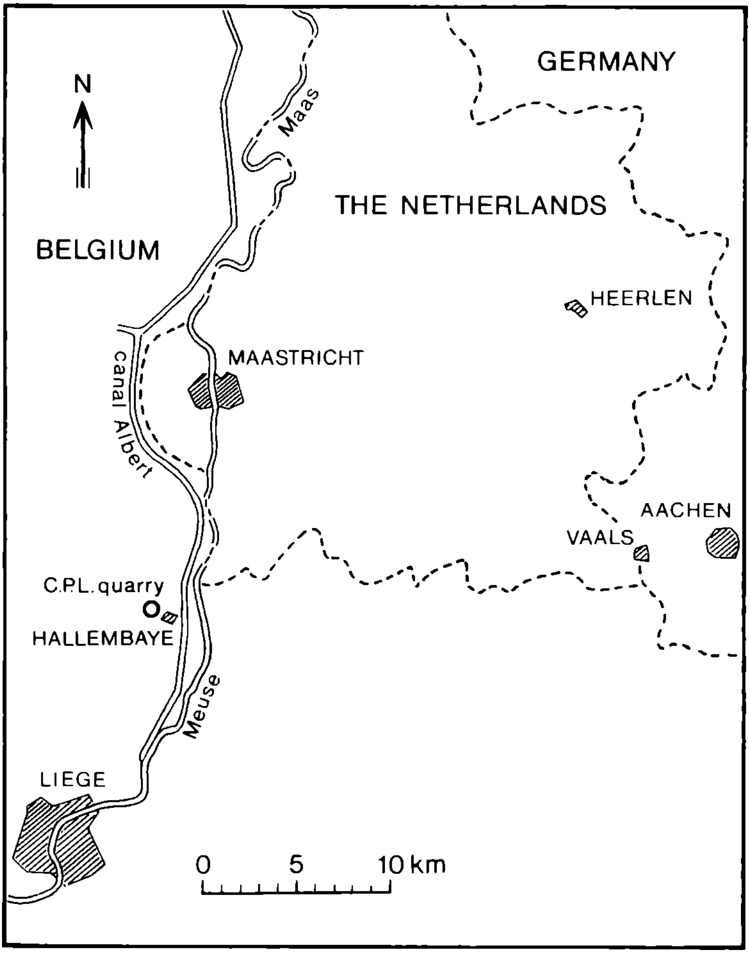

Fig. 1: Map of the Limburg area showing the location of the C.P.L. quarry at Hallembaye in Belgium. After ROBASZYNSKI et al. (1985).

4. Systematic Palaeontology

Morphology of the guard and terminology: The guard is usually the only part of the skeleton preserved; external and internal characters are used for taxonomic classification (Fig. 3).

The following characters are generally considered to be of taxonomic importance in describing Late Cretaceous belemnites belonging to Belemnitellidae PAVLOV: (1) size of

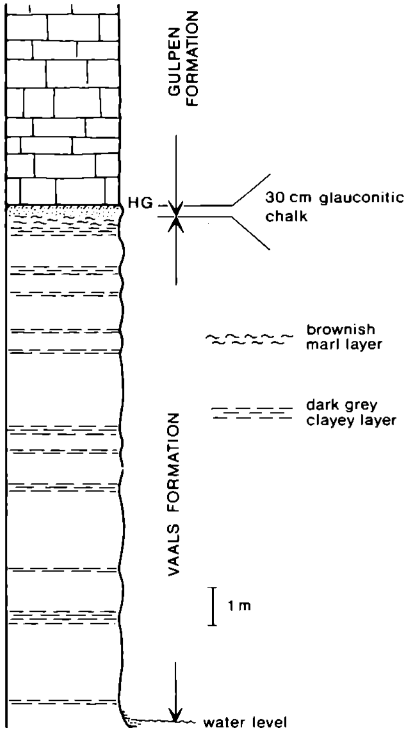

Fig. 2: Section of the Vaals Formation (earlier referred to as 'Smectite') and the lower part of the Gulpen Formation (earlier referred to as 'Craie blanche') in the C.P.L. quarry at Hallembaye, as measured by FS in 1958. The Vaals Formation is a glauconitic silt with clayey and marly beds, and the Gulpen Formation is a white chalk. The basal 30 cm of the Gulpen Formation is developed as a glauconitic chalk and is separated from the overlying part of the Gulpen Formation by a hard-ground (HG).

guard, (2) shape of guard, (3) structure of the anterior end, (4) surface markings, (5) internal characters, and (6) ontogeny. The characters were discussed recently by CHRISTENSEN (1986).

The term conellae is used descriptively for conical tubercles which may cover the wall of the alveolus or pseudoalveolus. In *B. praecursor* the conellae are covered by the 'white-layer' sensu CHRISTENSEN (1975a: 29).

The 'Riedel-Quotient' (ERNST 1964a) is the ratio of length of guard divided by depth of pseudoalveolus, and the 'Schlankheits-Quotient' (ERNST 1964a) is the ratio of length of guard divided by dorso-ventral diameter at the alveolar end.

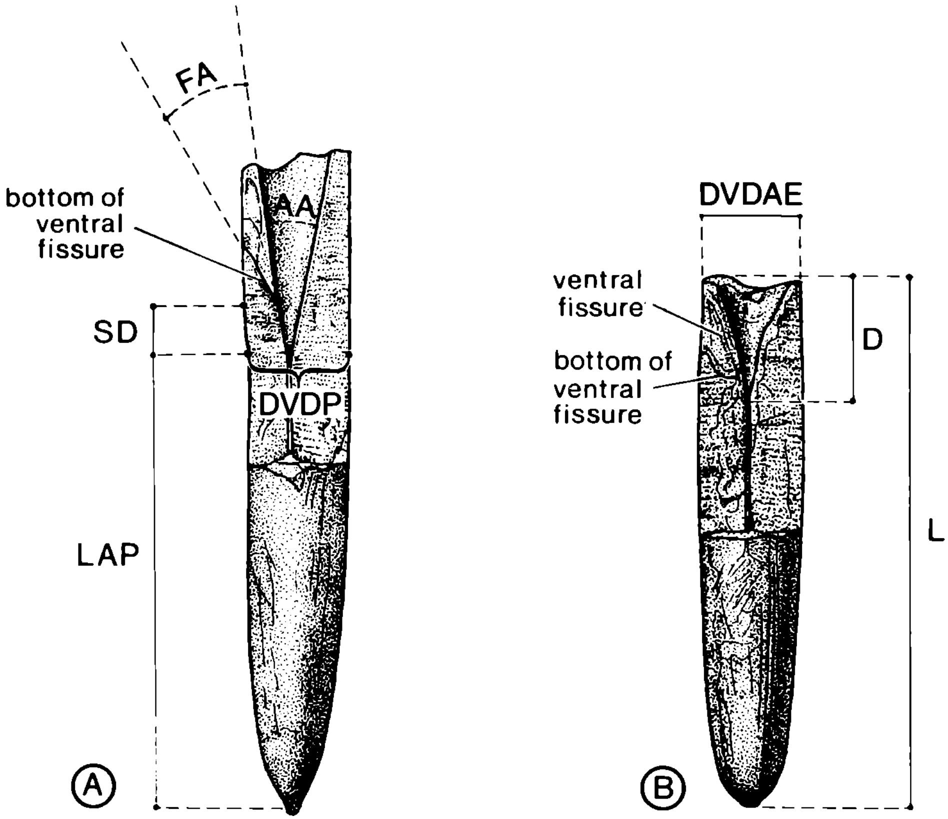

Fig. 3: Diagram showing the morphological elements of the guard.
A: *Belemnitella praecursor* STOLLEY. B: *Gonioteuthis quadrata quadrata* (BLAINVILLE). Both specimens were collected from the Vaals Formation, 100 cm beneath the boundary between the Vaals Formation and Gulpen Formation. AA = alveolar angle; FA = fissure angle; SD = Schatzky distance; DVDP = dorso-ventral diameter at protoconch; LAP = length from apex to protoconch; DVDAE = dorso-ventral diameter at alveolar end; L = length of guard; and D = depth of pseudoalveolus.

Measurements and abbreviations: A list of measured characters and abbreviations is given below (see also Fig. 3): Total length of guard (L), length from apex to protoconch (LAP), dorso-ventral diameter at protoconch (DVDP), lateral diameter at protoconch (LDP), dorso-ventral diameter at alveolar end, (DVDAE), Schatzky distance (SD), alveolar angle (AA), fissure angle (FA), 'Riedel-Quotient' (RQ), and 'Schlankheits-Quotient' (SQ).

Linear measurements were made with a vernier caliper to an accuracy of 0.1 mm, and angles were measured with a goniometer ocular fitted on a WILD stereomicroscope to an accuracy of 0.5°.

B i o m e t r i c m e t h o d s : The variability of the two belemnite species is analysed using univariate and bivariate statistical methods and is summarized by descriptive statistics, histograms, and scatter diagrams. The statistical methods and tests used in the present paper were fully discussed by CHRISTENSEN (1975a: 31--33).

T h e s p e c i e s c o n c e p t i n b e l e m n i t e s : The modern species concept in palaeontology is based on populations, rather than a few specimens (the so-called typological-morphological species concept). Species are studied by analysing the variation of homogeneous samples from restricted stratigraphic intervals using biometric methods. This concept has only recently been applied to Upper Cretaceous belemnites (i.a. ERNST 1964a, 1968, CHRISTENSEN 1971, 1973, 1974, 1975a, 1975b, 1986, SCHULZ 1979, and JARVIS 1980), and biometric studies have shown that many belemnite species and subspecies established by earlier workers are nothing but morphological variants.

CHRISTENSEN (1986) briefly discussed 'horizontal classification' versus 'vertical classification', and 'horizontal classification' was favoured because it can be considered as an approximation to the biological species concept; 'horizontal classification' is also used here.

ERNST (1964a, 1968) defined species of *Gonioteuthis* on the basis of analysis of samples from successive horizons ('horizontal classification'), but the stratigraphic ranges of the species were illustrated in diagrams using 'vertical classification'. In that way, two or three species of *Gonioteuthis* occur in the same horizon. This approach should be discouraged (CHRISTENSEN 1986).

Belemnitella praecursor STOLLEY, 1897
Pl. 1: 1–14; Pl. 2: 1–6; Pl. 3: 1–7

1896 *Belemnitella lanceolata* (SCHLOTHEIM): – BLACKMORE, p. 529, Pl. 16:1

1897 *Belemnitella praecursor* STOLLEY, p. 297, Pl. 3: 24

1906 *Belemnitella praecursor* STOLLEY: – MÜLLER & WOLLEMANN, p. 29, Pl. 6: 7–8

1912 *Belemnitella praecursor* STOLLEY: – ARKHANGELSKY, p. 604, Pl. 9: 1–2, 8, 22, Pl. 10: 33

1915 *Belemnitella praecursor* STOLLEY: – SINZOW, p. 143, Pl. 8: 13

1948 *Belemnitella praecursor* STOLLEY: – JELETZKY, p. 344, Figs. 5–6

1951 *Belemnitella praecursor* STOLLEY: – JELETZKY, p. 79, Pl. 1: 1–2

1955a *Belemnitella praecursor* STOLLEY var. **media** JELETZKY, p. 488, Pl. 56: 1–3, Pl. 57: 2–4, Pl. 58: 4

1955a *Belemnitella praecursor* STOLLEY var. *mucronatiformis* JELETZKY, p. 488, Pl. 56: 5, Pl. 58: 2

1955a *Belemnitella praecursor* STOLLEY s.l: – JELETZKY, p. 488, Pl. 56: 4

1955b *Belemnitella praecursor* STOLLEY: – JELETZKY, p. 876, Fig. 1

1959 *Belemnitella mucronata senior* NOWAK: – SCHMID, p. 239

1964 *Belemnitella praecursor* STOLLEY sensu lato: – JELETZKY, p. 287

1964 *Belemnitella praecursor* STOLLEY: – NAIDIN, p. 88, Pl. 1: 1

1964b *Belemnitella praecursor praecursor* STOLLEY: – ERNST, p. 190, Pl. 1: 1

1967 *Belemnitella praecursor mucronatiformis* JELETZKY: – SCHMID, p. 474

1967 *Belemnitella praecursor media* JELETZKY: – SCHMID, p. 474

1975a *Belemnitella praecursor* STOLLEY: – CHRISTENSEN, p. 30, Pl. 7: 5

1980 *Belemnitella praecursor* STOLLEY: – JARVIS, p. 891, Pl. 115: 1–3

1986 *Belemnitella praecursor* STOLLEY: – CHRISTENSEN, p. 31, Pl. 3: 4, Pl. 5: 1–2

Holotype: By monotypy the original of STOLLEY (1897, Pl. 3: 24). A cast of the holotype was figured by CHRISTENSEN (1986, Pl. 3: 4) (see also Pl. 3: 3–5, herein). The holotype came from the Broitzem quarry at Braunschweig, *Gonioteuthis granulata-quadrata* Zone of the basal Lower Campanian, and is housed in Geologisch-Paläontologisches Institut, Kiel, West Germany.

Measurements of the holotype: Length from apex to protoconch is 65.0 mm; dorso-ventral diameter at the protoconch is 16.2 mm; lateral diameter at the protoconch is 16.9 mm; Schatzky distance is ca. 10.00 mm; fissure angle is 6–7°; alveolar angle is 20°, and the bottom of the ventral fissure is almost straight (CHRISTENSEN 1986).

Material: 86 specimens collected by WKC, 50 specimens collected by FS, and 40 specimens on loan from the Natuurhistorisch Museum, Maastricht.

General description of sample from the C. P. L. quarry: The sample of *B. praecursor* consists of a growth series containing juvenile, adolescent and adult specimens, and represents an accumulation of several generations.

The length of well-preserved guards ranges up to 150 mm. In ventral view the guard is generally lanceolate with a constriction at the base of the ventral fissure, and in lateral view it is high conical. The guard is flattened over its entire length. The apical angle is acute in both juvenile and adult specimens, and the mucro is only slightly delimited.

The relationship between length from apex to protoconch and dorso-ventral diameter at the protoconch is allometric (see below); juvenile and adolescent specimens generally are slimmer than adult specimens. The ratio of the two characters varies from 3.1 (an average-sized specimen) to 5.9 (a juvenile specimen), being 3.6 – 4.6 in most specimens, and the mean value of the ratio is about 4.

The depth of the alveolus is about half the length of the guard in well-preserved specimens. The shape of the bottom of the ventral fissure is generally straight or almost straight, but it may also be straight with an outward bend, s-shaped, curved, or undulating. The walls of the alveolus may be covered by conellae. The fissure angle and the Schatzky distance are small, and the alveolar angle is about 20° (see univariate analysis below).

Adolescent and adult specimens have vascular markings, in addition to dorso-lateral depressions, dorso-lateral double furrows and longitudinal striae. The vascular markings are commonly weakly developed, and they are most prominent around the ventral fissure. The longitudinal striae are typically more distinct that the vascular markings. Juvenile specimens are, by and large, smooth.

Univariate analysis: The estimates of the statistical parameters are shown below.

B. praecursor from Hallembaye (W.K. CHRISTENSEN Coll.):

Character	N	$\bar{X}$	SD	CV	OR
LAP	46	60.9	11.8	19.4	20.1 – 79.2
DVDP	60	15.3	3.6	23.3	4.9 – 19.0
SD	57	6.4	1.3	20.9	4.2 – 10.2
FA	52	17.6	5.0	28.2	10.0 – 28.0
AA	59	20.1	0.9	4.3	18.0 – 22.0

N = number of specimens; $\bar{X}$ = mean value; SD = standard deviation;
CV = coefficient of variation; OR = observed range.

Histograms of the length from apex to protoconch, the Schatzky distance, and the fissure angle are shown in Fig. 4. The size-frequency distributions are asymmetrical, and they were tested for normality using the Kolmogorov-Smirnov test for goodness of fit. The Kolmogorov-Smirnov test is a powerfull non-parametric test, and the test statistic D is the maximum difference between the observed and expected cumulutative frequency distributions. It is discussed in detail by SIEGEL (1956: 47–52) and SOKAL & ROHLF (1969: 571–574). The result is shown below.

The holotype of *B. praecursor* and some specimens of *B. praecursor* from Russian Asia (Emba and west Kazakhstan) are also plotted in Fig. 5. The holotype of *B. praecursor* plots very close to the regression line for *B. praecursor*, whereas all the Russian specimens except for one plot below the regression line, indicating that they are generally slimmer than the Hallembaye specimens. The Russian specimens are further discussed below.

The scatter plot of a sample of *B. alpha* NAIDIN from Ringeleslätt in Scania is also shown in Fig. 5, as is regression line of this sample. The sample of *B. alpha* was described by CHRISTENSEN (1975a), and the estimates of the statistical parameters are given below.

B. alpha from Ringeleslätt (CHRISTENSEN 1975a):
DVDP = 2.2011 + 0.2441 LAP; N = 23; r = 0.9204; SD_a = 1.2355; SD_b = 0.0226; SD_{yx} = 1.2828.

The value of the correlation coefficient is very highly significant ($P<0.1\%$, with 21 degrees of freedom). A t-test on the y-intercept gave a value of 1.7816 with 21 degrees of freedom which is not significant ($P>5\%$), implying an isometric relationship of the two characters. This means that the ratio of the two characters does not change during growth. The ratio varies from 2.9–4.1, being 2.3–3.8 in most specimens, and the mean value is 3.5.

It is obvious from Fig. 5 that due to the allometric growth in *B. praecursor*, the difference between *B. praecursor* and *B. alpha* with respect to the shape of the guard is less in adult specimens that in juvenile and adolescent specimens.

Discussion: *B. praecursor* was established on the basis of only one specimen and characterized as being smooth (STOLLEY 1897). The critical internal characters were unknown because STOLLEY did not split the guard. The holotype was supposed to have been misplaced or lost during the Second World War (JELETZKY 1955a: 494), but it was found in 1976 in the Geologisch-Paläontologisches Institut, Kiel. The specimen was subsequently split by Dr. M.-G. SCHULZ, Kiel, who supplied the measurements of the internal characters listed above.

JELETZKY (1955a) fully discussed the concept of *B. praecursor*, based mainly on Russian material and some specimens from England and Sweden. He emended the diagnosis of *B. praecursor* and also included specimens with more or less developed vascular markings and a more or less distinct mucro in *B. praecursor*. He distinguished three varieties of *B. praecursor*: var. *praecursor*, var. *media* JELETZKY, and var. *mucronatiformis* JELETZKY, but failed to present appropriate biometrical analysis and/or differential diagnosis of the varieties. According to JELETZKY, var. *praecursor* is smooth; var. *mucronatiformis* has a fairly sculptured guard with vascular markings and a more or less distinct mucro; and var. *media* is a morphologically intermediate form between var. *praecursor* and var. *mucronatiformis*. He stated that the varieties ". . are only morphological varieties of the same specific type (Parts of the same populations). ." (JELETZKY 1955a: 482). The varieties are, however, to be treated as subspecies, following § 45g of the 3rd Edition of the Code from 1985, because the taxa have been used as subspecies in papers published before 1985.

The sample from Hallembaye is assigned to *B. praecursor* and subspecies are not recognized. It should however, be stated that adult specimens with a smooth guard do not occur in the sample.

B. praecursor praecursor is very rare in NW-Europe, and according to the knowledge of the present authors, it has only been recorded from West Germany (STOLLEY 1897, Pl. 3: 24; MÜLLER & WOLLEMANN 1906, Pl. 6: 8; ERNST 1964b, Pl. 1: 1).

One of us (WKC) has studied eleven specimens of *B. praecursor* from the basal Lower Campanian of Russian Asia (ex Prof. D.P. NAIDIN's Coll.). These specimens are, by and large, more slender than the specimens from NW Europe (see Fig. 5), and the Russian specimens may represent a geographical subspecies. Examination of additional material, however, is necessary in order to solve this problem.

Affinities: *B. praecursor* is closely allied to *B. alpha* NAIDIN from the lower and middle Lower Campanian and *B. mucronata* (SCHLOTHEIM) from the uppermost Lower Campanian – Upper Campanian. The sample of *B. praecursor* from Hallembaye was compared to a sample of *B. alpha* from Sweden and three samples of *B. mucronata* from Sweden and W. Germany. The sample of *B. alpha* came from Ringeleslätt (basal Lower Campanian) in the Kristianstad Basin and was described by CHRISTENSEN (1975a, 1986). The samples of *B. mucronata* came from Ignaberga (uppermost Lower Campanian) and Balsvik (lower Upper Campanian) in the Kristianstad Basin (see CHRISTENSEN 1975a), and the Germania IV quarry (lower Upper Campanian) at Misburg near Hannover (see CHRISTENSEN et al. 1975).

The surface sculpture of *B. praecursor* is very similar to that of *B. alpha*; both species have weakly developed vascular markings and the longitudinal striae are more prominent than the vascular markings. The t-tests on the mean values of length from apex to protoconch, the Schatzky distance, and the fissure angle show that the mean values differ significantly at the 5% level. The regression lines of the two samples were also compared. No significant differences were found of the variances and slopes of the two lines. A t-test on the positions, however, gave a value of 7.63 with 65 degrees of freedom, which is very highly significant ($P<0.1\%$). *B. praecursor* thus differs from *B. alpha* by being more slender, attaining a larger size of the guard, having a smaller Schatzky distance, and a larger fissure angle. In addition, the relationship of length from apex to protoconch vs dorso-ventral diameter at the protoconch is allometric in *B. praecursor* and isometric in *B. alpha*.

Although the two species differ with respect to several critical characters, it is not possible on the basis of only a few specimens to assign them safely to either *B. alpha* or *B. praecursor*, because the range of variation overlaps. One needs a sample of a certain size, say 15–20 specimens, to make a reliable determination.

B. praecursor differs from *B. mucronata* by having weakly developed vascular markings, lacking a well-defined mucro, being larger, and more slender. The Schatzky distance is very similar in the two species. The fissure angle in samples of *B. mucronata* from the uppermost Lower Campanian-basal Upper Campanian and *B. praecursor* is also very similar. Samples of *B. mucronata* from the middle Upper Campanian generally have larger fissure angles than *B. praecursor*.

Distribution: *B. praecursor* has been recorded from Northern Ireland across England, France, Belgium, northern Germany, Poland to Russia.

B. praecursor occurs in Western Germany in the *G. granulataquadrata* Zone and the overlying *I. lingua/G. quadrata* Zone of the basal Lower Campanian (ERNST 1964b) (Fig. 6). A single specimen has also been collected from the middle Lower Campanian *G. senonensis* Zone of Lägerdorf (M.-G. SCHULZ, Kiel, pers. comm.). In southern England, it occurs in the middle Lower Campanian *Hagenowia blackmorei* Horizon (see Fig. 6). JARVIS (1980) recorded the species from the middle Lower Campanian phosphatic chalk of the Anglo-Paris Basin in France. In Northern Ireland it was recorded from the middle Lower Campanian Boheeshane A Chalk by FLETCHER & WOOD (1978). In Russia, *B. praecursor* is said to appear in the uppermost Santonian and continue into the lower and middle Lower Campanian (NAIDIN & KOPAEVICH 1977, NAIDIN 1979, 1983). The sample of *B. praecursor* from the Vaals Formation in the C.P.L. quarry at Hallembaye is from the lower part of the *I. lingua/G. quadrata* Zone of the basal Lower Campanian (see below).

Gonioteuthis quadrata quadrata (BLAINVILLE, 1827)
P. 3: 8–11

Holotype: By monotypy the original of BLAINVILLE (1827, Pl. 1: 9).

Material: 73 specimens collected by WKC, 9 collected by FS, in addition to 37 specimens obtained on loan from the Natuurhistorisch Museum, Maastricht.

Remarks: The evolutionary lineage of *Gonioteuthis* BAYLE, in ascending order: *G. westfalica praewestfalica* ERNST & SCHULZ, *G. w. westfalica* (SCHLÜTER), *G. westfalicagranulata* (STOLLEY), *G. granulata* (BLAINVILLE), *G. granulataquadrata* (STOLLEY), *G. q. quadrata* (BLAINVILLE), and *G. quadrata gracilis* (STOLLEY), was studied in detail by STOLLEY (1897, 1916, 1930), ERNST (1963a, 1963b, 1964a, 1964b, 1966, 1968), ERNST & SCHULZ (1974), CHRISTENSEN (1975a, 1975b, 1986), and JARVIS (1980).

The *Gonioteuthis* lineage provides a valuable tool for biostratigraphic purposes. It is, however, necessary to analyse homogeneous samples of a certain size in order to make a

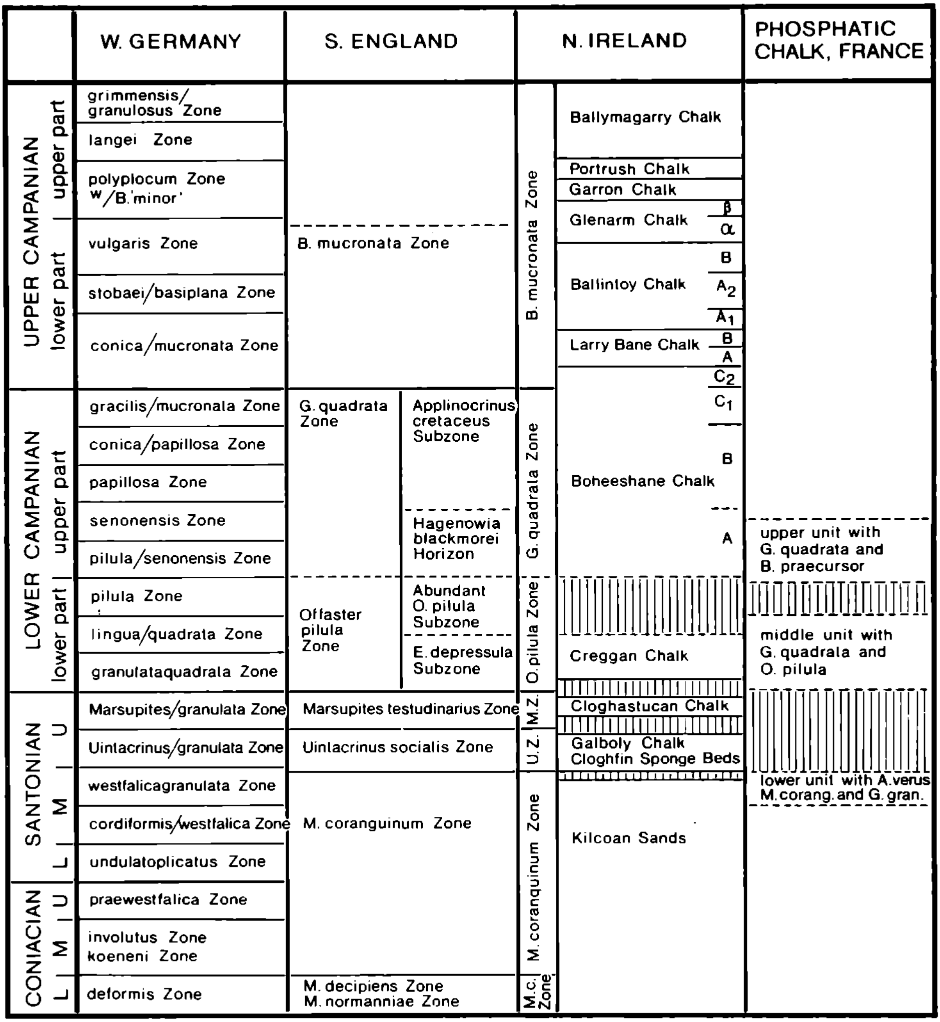

Fig. 6: Stratigraphic correlation diagram of the Coniacian – Maastrichtian. Sources: SCHULZ (1978), ERNST et al. (1979), and ERNST & SCHULZ (1980) for western Germany; BAILEY et al. (1983) for southern England; FLETCHER (1977) and FLETCHER & WOOD (1978, 1982) for Northern Ireland; and JARVIS (1980) for France. Modified from CHRISTENSEN (1986).

reliable determination, and limited material has only little stratigraphic value (ERNST 1964a, CHRISTENSEN 1975a, 1986).

In studies of *Gonioteuthis*, the following characters are of importance: (1) length of guard, (2) length of guard vs depth of pseudoalveolus, and (3) length of guard vs dorso-ventral diameter at alveolar end.

Biometry: A sample of *Gonioteuthis* consisting of 73 specimens was analysed by univariate and bivariate biometric methods. Three complete specimens were excluded from the analysis because the structure of the anterior end of these specimens is aberrant.

Univariate analysis:

Character	N	X	SD	CV	OR
L	60	67.3	7.2	10.7	52.0 – 80.3
RQ	58	4.5	0.5	11.1	3.5 – 5.9
SQ	58	5.7	0.5	8.8	4.5 – 6.7

Histograms of length of guard, 'Riedel-Quotient', and 'Schlankheits-Quotient' are shown in Fig. 7. The size-frequencey distributions were tested for normality using the

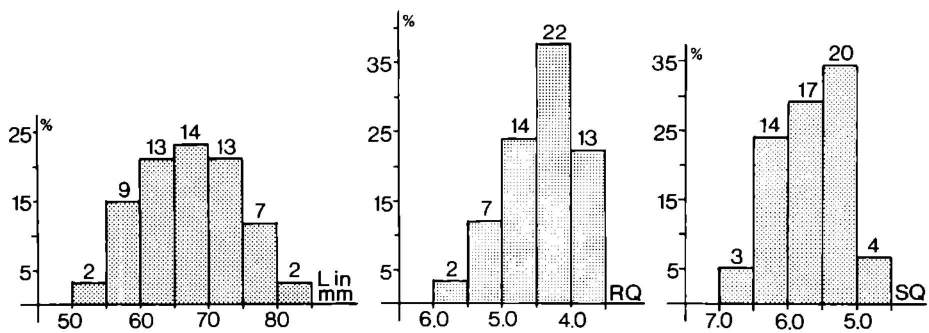

Fig. 7: Histograms of length of guard (L), 'Riedel-Quotient' (RQ), and 'Schlankheits-Quotient' (SQ) for *G. q. quadrata* from the C.P.L. quarry at Hallembaye. The numbers above the bars are the actual number of specimens.

Kolmogorov-Smirnov test for goodness of fit, and none of the distributions differed significantly from normality at the 5% level (see below).

Kolmogorov-Smirnov test:

Character	N	D	Probability
L	60	0.0467	$P > 50\%$
RQ	58	0.0986	$P > 50\%$
SQ	58	0.1019	$P > 50\%$

It should be emphasized that in contrast to the sample of *B. praecursor* juvenile specimens are absent in the *Gonioteuthis* sample.

Bivariate analysis: The scatter plots of length of guard vs depth of pseudoveolus and length of guard vs dorso-ventral diameter at the alveolar end are shown in Fig. 8, as are the regression lines.

The equations of the regression lines are as follows.

(1) $D = -4.6948 + 0.2970\ L$; $N = 58$; $r = 0.8192$; $SD_a = 1.8903$; $SD_b = 0.0280$; $SD_{yx} = 1.5332$.

(2) $DVDAE = -2.4293 + 0.2136\ L$; $N = 58$; $r = 0.8326$; $SD_a = 1.2636$; $SD_b = 0.0187$; $SD_{yx} = 1.0293$.

The values of the correlation coefficients are very highly significant ($P < 0.1\%$, with 56 degrees of freedom).

In the first analysis, the t-test on the y-intercept gave a value of 2.4836, with 56 degrees of freedom, which is significant ($2\% > P > 1\%$). The relationship of the two variates is thus allometric, and adult specimens generally have a deeper pseudoalveolus than juvenile specimens. Due to the allometric relationship, it is not legitimate to calculate the mean 'Riedel-Quotient' as done above. The mean 'Riedel-Quotient' was computed, nevertheless, because the growth is not strongly allometric, and in order to facilitate comparison with German samples of *Gonioteuthis* as described by ERNST (1964a, 1964b).

In the second analysis, the t-test on the y-intercept gave a value of 1.9225, with 56 degrees of freedom, which is not significant ($10\% > P > 5\%$), indicating an isometric relationship of the variates.

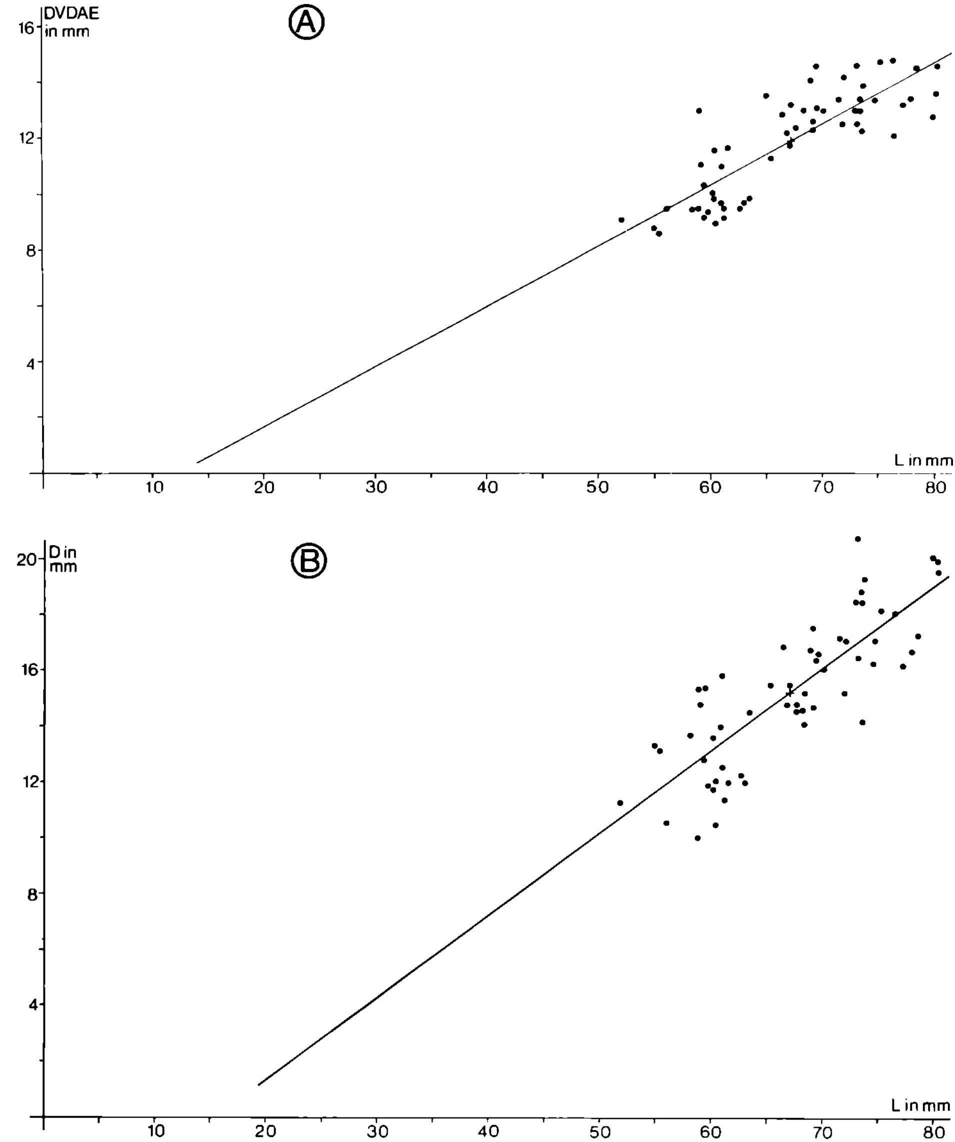

Fig. 8: Scatter plots and regression lines, fitted by the least squares method, for *G.q. quadrata* from the C.P.L. quarry at Hallembaye.
A: Length of guard (L) versus dorso-ventral diameter at the alveolar end (DVDAE).
B: Length of guard (L) versus depth of pseudoalveolus (D). + = mean value.

On the basis of the univariate and bivariate analyses the sample from Hallembaye is regarded as homogeneous, although it should be stressed that juvenile specimens are absent.

Comparison: The sample of *Gonioteuthis* from Hallembaye was compared to three samples of *Gonioteuthis* from Germany.

(1) *G. granulataquadrata* from the Weinberg brickyard, situated immediately west of Braunschweig (cf. ERNST 1964a: 120, 1968: 263–265, 278; CHRISTENSEN 1975a; 38–39, 1975b: 131). The sample is from the basal Lower Campanian, *G. granulataquadrata* Zone. The measurements were kindly placed at our disposal by G. ERNST.

Character	N	$\bar{X}$	SD	CV	OR
L	45	66.1	8.5	12.9	48.5 – 84.0
RQ	45	5.3	0.5	10.4	4.4 – 6.3
SQ	45	5.5	0.4	7.5	4.8 – 6.9

(1) $D = 1.0295 + 1.1760\ L$; $N = 45$; $r = 0.7404$; $SD_a = 1.6233$; $SD_b = 0.0244$; SD_{yx} 1.3699.

(2) $DVAE = -1.1019 + 0.2008\ L$; $N = 45$; $r = 0.9051$; $SD_a = 0.9584$; $SD_b = 0.0144$; $SD_{yx} = 0.8088$.

The correlation coefficients are very highly significant ($P < 0.1\%$, with 43 degrees of freedom). The t-tests on the y-intercepts gave values, which are not significant at the 5% level. The relationships of length of guard vs depth of pseudoalveolus and length of guard vs dorsoventral diameter at alveolar end are thus isometric.

(2) *G. quadrata quadrata* from the Bremer brickyard, situated about 12 km northwest of Essen. This locality was discussed by ERNST (1964a, 1964b) and placed in the lower part of the *I. lingua/G. quadrata* Zone. Measurements of length of guard and depth of pseudoalveolus of a sample measured in 1972 were placed at our disposal by G. ERNST.

Character	N	$\bar{X}$	SD	CV	OR
L	38	67.3	6.4	9.5	58.5 – 82.5
RQ	38	4.6	0.6	13.1	3.7 – 6.3

(1) $D = -3.1563 + 0.2687\ L; N = 38; r = 0.6924; SD_a = 3.1534; SD_b = 0.0467; SD_{yx} = 1.8027.$

The correlation coefficient is very highly significant ($P < 0.1\%$, with 36 degrees of freedom). A t-test on the y-intercept gave a value of 1.0009 with 36 degrees of freedom, which is not significant at the 5% level. The relationship of the two variates is thus isometric. The mean 'Schlankheits-Quotient' was not computed, because measurements of the dorso-ventral diameter were not available. ERNST (1964a), however, reported that the mean 'Schlankheits-Quotient' of another sample from the Bremer brickyard is 5.6.

(3) *G. quadrata quadrata* from the upper *I. lingua/G. quadrata* Zone of the Höver quarry near Hannover (cf. ERNST 1964a: 119; CHRISTENSEN 1975a: 39). The measurements were placed at our disposal by G. ERNST.

Character	N	X	SD	CV	OR
L	24	60.3	10.5	17.4	41.0 – 78.0
RQ	24	4.0	0.5	12.2	2.8 – 4.9
SQ	24	5.9	0.5	9.9	5.1 – 6.8

(1) $D = -0.8883 + 0.2685\ L; N = 24; r = 0.7982; SD_a = 2.6404; SD_b = 0.0432; SD_{yx} = 2.1657.$

(2) $DVDAE = -1.8504 + 0.2018\ L; N = 24; r = 0.9193; SD_a = 1.1258; SD_b = 0.0184; SD_{yx} = 0.9234.$

The correlation coefficients are very highly significant ($P < 0.1\%$, with 22 degrees of freedom). The t-tests on the y-intercepts gave values which are not significant at the 5% level, indicating an isometric relationship of the variates in both analyses.

The size of guard: The mean values of length of guard of the samples from Hallembaye, Weinberg and Bremer are of little taxonomic value because juvenile specimens are absent in these samples. According to ERNST (1964a) the length of the guard of the *Gonioteuthis* lineage reaches a maximum (up to 85–90 mm) in *G. granulata-quadrata* and *G. quadrata* from the lower and middle Lower Campanian. On the basis of the maximum length, the sample from Hallembaye are thus from the lower-middle Lower Campanian.

Length of guard vs depth of pseudoalveolus (Fig. 9B): The regression line of the Hallembaye samples was compared to regression lines of the samples from Weinberg, Bremer, and Höver. As regards Hallembaye and Weinberg, a highly

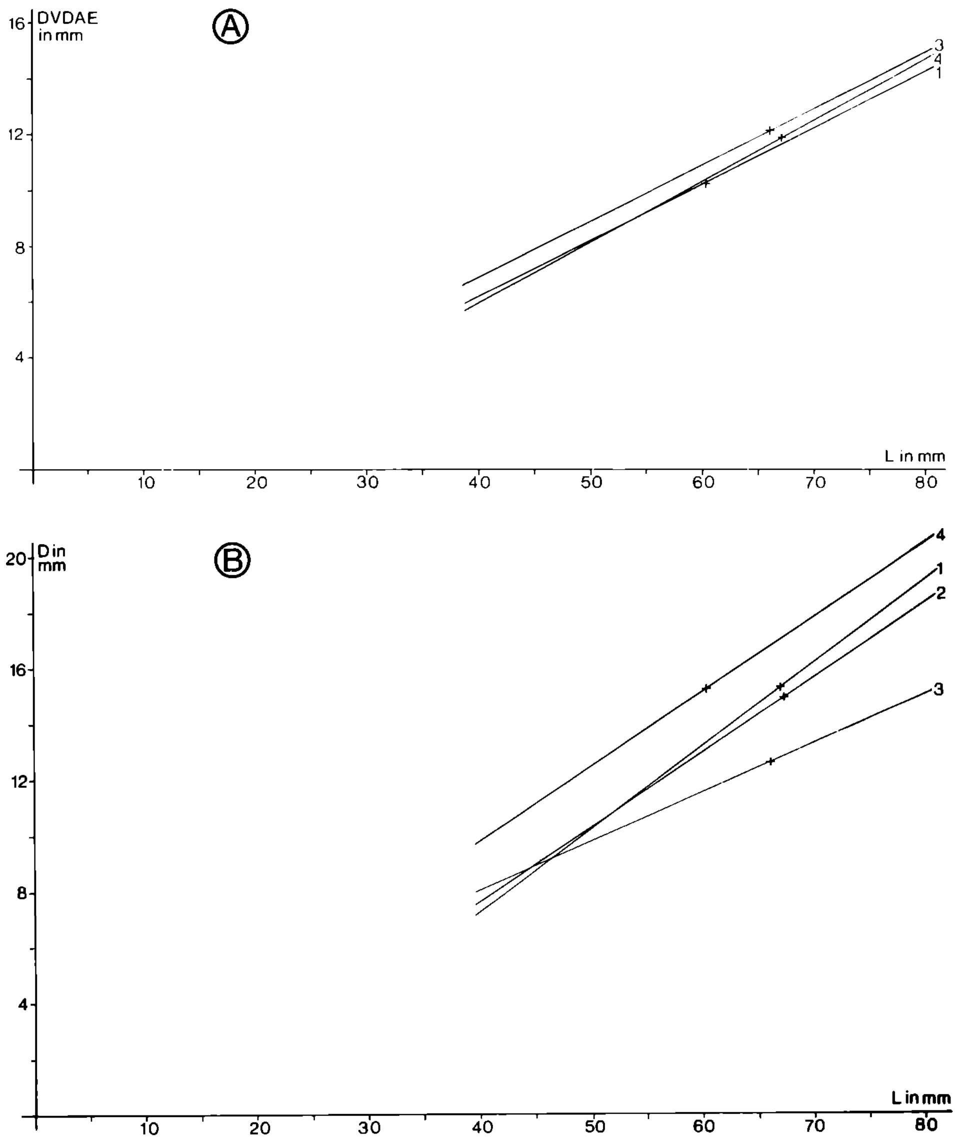

Fig. 9: Regression lines fitted by the least squares method. A: Length of guard (L) versus dorso-ventral diameter at the alveolar end (DVDAE). B: Length of guard (L) versus depth of pseudoalveolus (D). + = mean values. 1: *G.q. quadrata* from the C.P.L. quarry at Hallembaye. 2: *G.q. quadrata* from Bremer's brickyard. 3: *G. granulataquadrata* from the Weinberg brickyard. 4: *G.q. quadrata* from the upper *I. lingua/G. quadrata* Zone of Höver.

significant difference was found between the slopes (0.5% > P > 0.1%, with 99 degrees of freedom). The specimens from Hallembaye generally have a deeper pseudoalveolus than the specimens from Weinberg. This is especially distinct in adult specimens owing to the allometric relationship of the Hallembaye sample. The sample from Hallembaye is virtually identical to the sample from Bremer, and tests showed that the variances, slopes, and positions do not differ at the 5% level. The comparison of the Hallembaye and Höver samples showed that the difference between the positions of the two lines is very highly significant (P < 1%, with 78 degrees of freedom). The specimens from Hallembaye generally have a shallower pseudoalveolus than the Höver specimens.

Length of guard vs dorso-ventral diameter at the alveolar end (Fig. 9A): The specimens from Hallembaye are generally slimmer than the specimens from Weinberg. With respect to the slopes, the samples do not differ significantly (60% > P > 50%, with 99 degrees of freedom), but the positions are significantly different (2% > P > 1%, with 99 degrees of freedom). ERNST (1964a) reported that the mean 'Schlankheits-Quotient' of a sample from Weinberg was 5.6. This mean value is very close to the mean value of 5.7 for the Hallembaye sample. The comparison of the Hallembaye and Höver samples showed that the slopes and positions do not differ significantly at the 5% level.

Conclusions: The sample of *Gonioteuthis* from Hallembaye cannot be differentiated from the sample of *G.q. quadrata* from Bremer with respect to size and shape of guard and depth of pseudoalveolus. The Hallembaye specimens generally have a deeper pseudoalveolus and are more slender than *G. granulataquadrata* from Weinberg, and have a more shallow pseudoalveolus than *G.q. quadrata* from Höver. The sample of *Gonioteuthis* from Hallembaye is therefore referred to *G.q. quadrata* and is regarded to be from the Lower Campanian, lower part of the *I. lingua/G. quadrata* Zone *sensu germanico*, as is the sample from Bremer.

5. The Belemnite Faunas of the lower – middle Lower Campanian

Four genera of *Belemnitellidae* occur in the lower – middle Lower Campanian: *Actinocamax* MILLER, *Gonioteuthis* BAYLE, *Belemnellocamax* NAIDIN, and *Belemnitella* D'ORBIGNY (cf. CHRISTENSEN 1976, 1986). In western Europe *Actinocamax* is restricted to one species, *A. verus* MILLER; *Gonioteuthis* to two species, *G. granulataquadrata* and *G. quadrata; Belemnellocamax* to one group, *B.* ex gr. *grossouvrei* (JANET); and *Belemnitella* to two species, *B. praecursor* and *B. alpha* (cf. CHRISTENSEN 1976, 1986).

The belemnite assemblage of the Vaals Formation is characterized by: (1) it only consists of *B. praecursor* and *G.q. quadrata*, (2) *B. praecursor* is more common here than elsewhere, and (3) the sample of *B. praecursor* consists of all growth stages, while juvenile specimens are absent in the *G.q. quadrata* sample.

The absence of *B.* ex gr. *grossouvrei* in der Vaals Formation may be explained by the fact that this group is very rare (CHRISTENSEN 1976, 1986). *A. verus* is common in near-shore, shallow water sediments of basal Early Campanian age in southern Sweden (CHRISTENSEN 1986), the Lower Saxony Basin at Braunschweig (MÜLLER & WOLLEMANN 1906, ERNST 1968), the Cretaceous Subhercynian Basin in East Germany (ULBRICH 1971), and the Bottrop Marl of the Münster Basin (ERNST 1964b). In off-shore chalks of England, France, and West Germany the species is virtually restricted to the Upper Santonian (ERNST & SCHULZ 1974, FLETCHER & WOOD 1978, JARVIS 1980). The absence of *A. verus* from the Vaals Formation is engimatic, and it may have been ousted by *B. praecursor*.

During the late Coniacian – Lower Campanian, two belemnite subprovinces were recognized within the North European palaeobiogeographic Province: the Central Russian Subprovince characterized by the *Belemnitella* stock (including *'Actinocamax' lundgreni* STOLLEY) and the Central European Subprovince characterized by the *Gonioteuthis* stock (CHRISTENSEN 1975a, 1976). The C.P.L. quarry at Hallembaye is situated in the Central European Subprovince, and *B. praecursor* is more common here than elsewhere in this subprovince. It is roughly estimated that *B. praecursor* accounts for about 40% of the belemnite assemblage in the Vaals Formation. *B. praecursor* is extremely rare in West Germany (ERNST 1964b), East Germany (ULBRICH 1971), and Poland (KONGIEL 1962). In the middle Lower Campanian phosphatic chalks of northern France, *B. praecursor* occurs together with *G. quadrata*, but only constitutes 3–4% of the belemnite assemblage (JARVIS 1980).

CHRISTENSEN (1976) regarded the late Coniacian – Lower Campanian representatives of the *Belemnitella* stock in the Central European Subprovince as stray specimens or stray populations. The presence of all growth stages of *B. praecursor* in the Vaals Formation in addition to the fact that it occurs commonly, seems to indicate that *B. praecursor* lived and reproduced in that area.

CHRISTENSEN (1976) analysed the facies distribution of Upper Cretaceous belemnites of NW Europe and concluded that populations from near-shore sediments are characterized by containing all growth stages, in contrast to populations from off-shore chalks which generally consist of adults. The sample of *G. q. quadrata* differs from this pattern in that juvenile specimens are absent.

6. Conclusions

A large sample of *B. praecursor* from the Vaals Formation of the C.P.L. quarry at Hallembaye in Belgium is analysed using univariate and bivariate biometric methods in order to study the variation of critical characters. *B. praecursor* is closely allied to *B. alpha* and *B. mucronata*. The surface sculpture of *B. praecursor* and *B. alpha* is very similar, but *B. praecursor* differs from *B. alpha* by being more slender, attaining a larger size of the guard, having a smaller Schatzky distance, and a larger fissure angle. In addition, the relationship of length from apex to protoconch vs dorso-ventral diameter at the protoconch is allometric in *B. praecursor* and isometric in *B. alpha*. *B. praecursor* differs from *B. mucronata* by being larger, having weakly developed vascular markings, and lacking a well-defined mucro. Moreover, *B. praecursor* differs from *B. mucronata* from the middle Upper Campanian by having a smaller fissure angle.

B. praecursor occurs together with *G.q. quadrata*, which is also analysed by biometric methods. The sample from Hallembaye is compared to German samples of *Gonioteuthis* from well-known stratigraphic levels, and the comparisons show that the sample of *G.q. quadrata* is from the lower Lower Campanian, lower part of the *I. lingua/G. quadrata* Zone *sensu germanico*. The belemnite-bearing upper part of the Vaals Formation in the Hallembaye quarry is thus from the lower Lower Campanian.

The belemnite assemblage of the Vaals Formation is unusual in that it only consists of two species, *B. praecursor* and *G.q. quadrata*, and the former is more common here than elsewhere in the Central European Subprovince. Moreover, the size-frequency distributions show that juvenile specimens are absent in the sample of *G.q. quadrata*, which is at variance with observations from other belemnite populations from near-shore, shallow water deposits.

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PLATE 1 – 3

Plate 1

Belemnitella praecursor STOLLEY from the C.P.L. quarry at Hallembaye. All figures are of natural size unless otherwise stated. The specimens are coated with ammonium chloride except Fig. 7.

Figs. 1–3:	Juvenile specimen. 1: Dorsal view. 2: Lateral view. 3: Ventral view. MGUH 17520.
Fig. 4:	Juvenile specimen in ventral view. MGUH 17521.
Figs. 5–7:	Specimen with an average shape. 5: Lateral view. 6: Ventral view. 7: View of the split anterior end showing the internal features, x 1.5. MGUH 17522.
Figs. 8–10:	Specimen with an average shape. 8: Dorsal view. 9: Lateral view. 10: Ventral view. MGUH 17523.
Figs. 11–14:	Specimen with an average shape. 11: Dorsal view. 12: Lateral view. 13: Ventral view. View of the split anterior end, x 1.5. MGUH 17524.

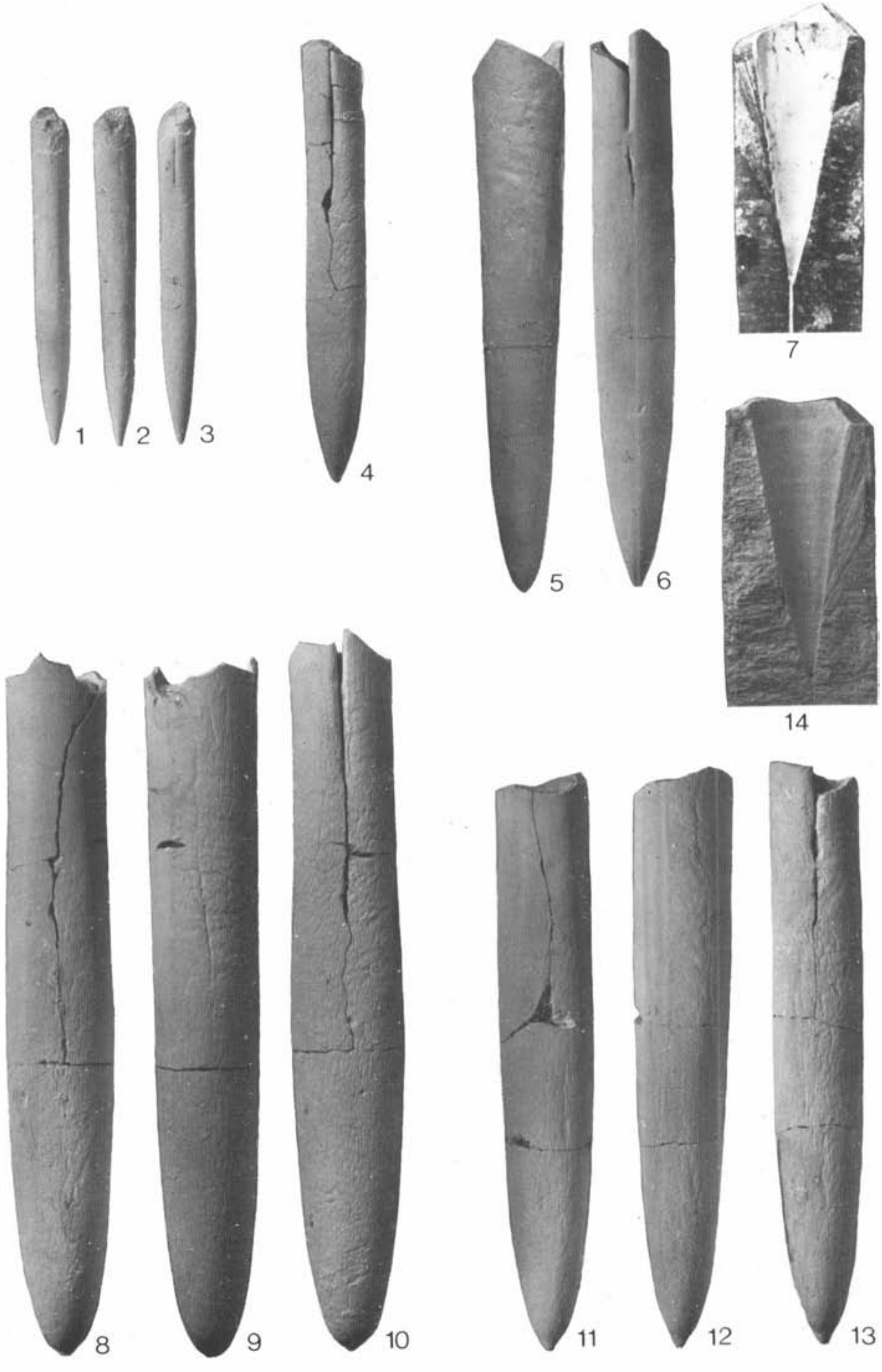
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Plate 2

Belemnitella praecursor STOLLEY from the C.P.L. quarry at Hallembaye. All figures are of natural size unless otherwise stated. Specimens coated with ammonium chloride except Fig. 4.

Figs. 1–4:	A slender specimen. 1: Dorsal view. 2: Lateral view. 3: Ventral view. 4: View of the split anterior end showing the internal features, x 1.5. MGUH 17525.
Figs. 5–8:	A large specimen with an average shape. 5: Dorsal view. 6: Lateral view. 7: Ventral view. 8: View of the anterior end showing the internal features, x 1.5. MGUH 17526.

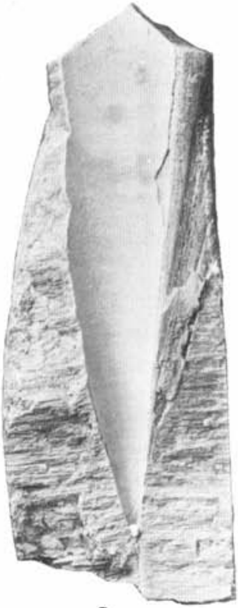

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Plate 3

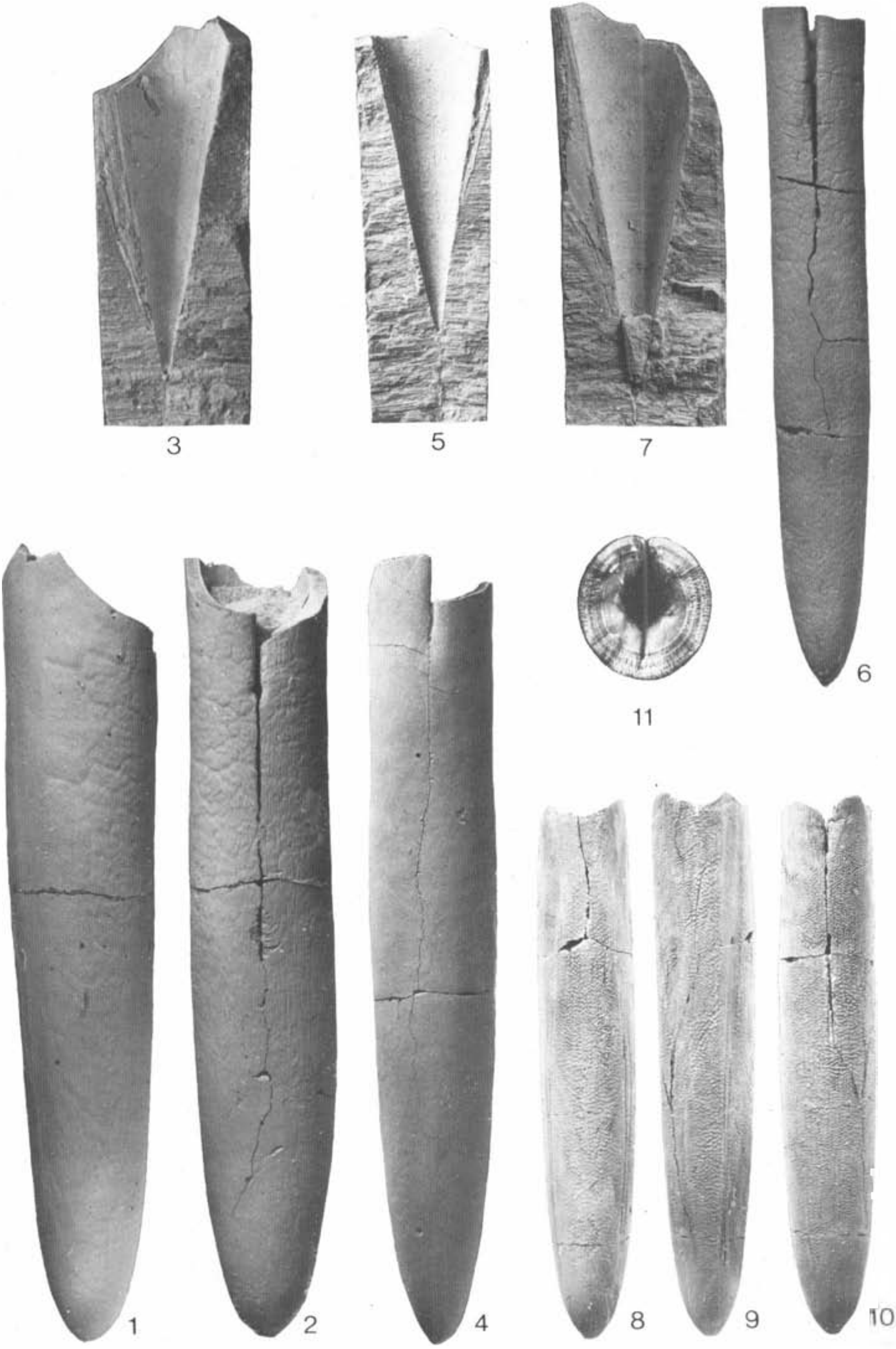
All figures are of natural size unless otherwise stated. All specimens are coated with ammonium chloride.

Figs. 1–3: *Belemnitella praecursor* STOLLEY from the C.P.L. quarry at Hallembaye. A large stout specimen. 1: Lateral view. 2: Ventral view. 3: View of the split anterior end showing the internal features. MGUH 17527.

Figs. 4–5: *Belemnitella praecursor* STOLLEY from the Broitzem quarry at Braunschweig. *Gonioteuthis granulataquadrata* Zone of the basal Campanian. Cast of holotype. 4: Ventral view. 5: View of the split anterior end showing internal features.

Figs. 6–7: *Belemnitella praecursor* STOLLEY from the C.P.L. quarry at Hallembaye. Medium-sized specimen with an average shape. 6: Ventral view. 7: View of the split anterior end showing the internal features, x 1.5. MGUH 17528.

Figs. 8–11: *Gonioteuthis quadrata quadrata* (BLAINVILLE) from the C.P.L. quarry at Hallembaye. 8: Dorsal view. 9: Lateral view. 10: Ventral view. 11: View of the anterior end, x 1.5. MGUH 17529.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