

PALAEOBIOLOGY OF UPPER CRETACEOUS BELEMNITES FROM THE PHOSPHATIC CHALK OF THE ANGLO-PARIS BASIN

by IAN JARVIS

ABSTRACT. The phosphatic chalks of northern France exhibit a tripartite belemnite biostratigraphy, with *Actinocamax verus* Miller at their base, *Goniot euthis* ex gr. *quadrata* in their upper portions, and *G. quadrata quadrata* and *Belemnitella praecursor* Stolley at their summit. *G. granulata* (Blainville) is identified from isolated specimens collected from the base of the sequences; *G. granulata quadrata* (Stolley) is recognized within 'populations' from the summit of phosphatic chalks. Principal component factor analysis suggests that variation in guard morphology may be attributed to differences in guard size and to the evolutionary stage reached by individuals within the gradualistic series formed by the genus *Goniot euthis*. Heterogeneity in one sample is the result of mixing of juvenile and mature populations caused by a catastrophic event, probably a storm. The presence of juveniles in all samples indicates a near-shore environment which was the normal habitat of belemnites. Hardgrounds show associated concentrations of belemnites because of greater food availability and their suitability as breeding sites.

BELEMNITES occur throughout the Santonian to early Campanian sequences of the Anglo-Paris Basin, but their rarity may be measured by the observations of Rowe (1908, p. 311) who obtained only ten specimens of *Goniot euthis* from the entire Campanian section on the Isle of Wight during more than two months' intensive collecting. Similarly, Brydone (1914) stated that only thirteen accurately located and identifiable specimens of *Goniot euthis* had previously been recorded from the Chalk of Hampshire and Sussex. The infrequency of belemnites in soft white chalks of this age has been noted by other authors in sequences outside the Anglo-Paris Basin (e.g. Ernst 1964; Christensen 1976b). Belemnites, in particular *Goniot euthis* and *Actinocamax verus* Miller are, however, common and at some levels extremely abundant in the phosphatic chalk lithofacies. Consequently, while the sporadic occurrence of belemnites in soft white chalks has led to the inapplicability of population analyses, material from phosphatic chalks provides a unique opportunity to examine accurately located 'populations', rather than isolated specimens.

PHOSPHATIC CHALK STRATIGRAPHY

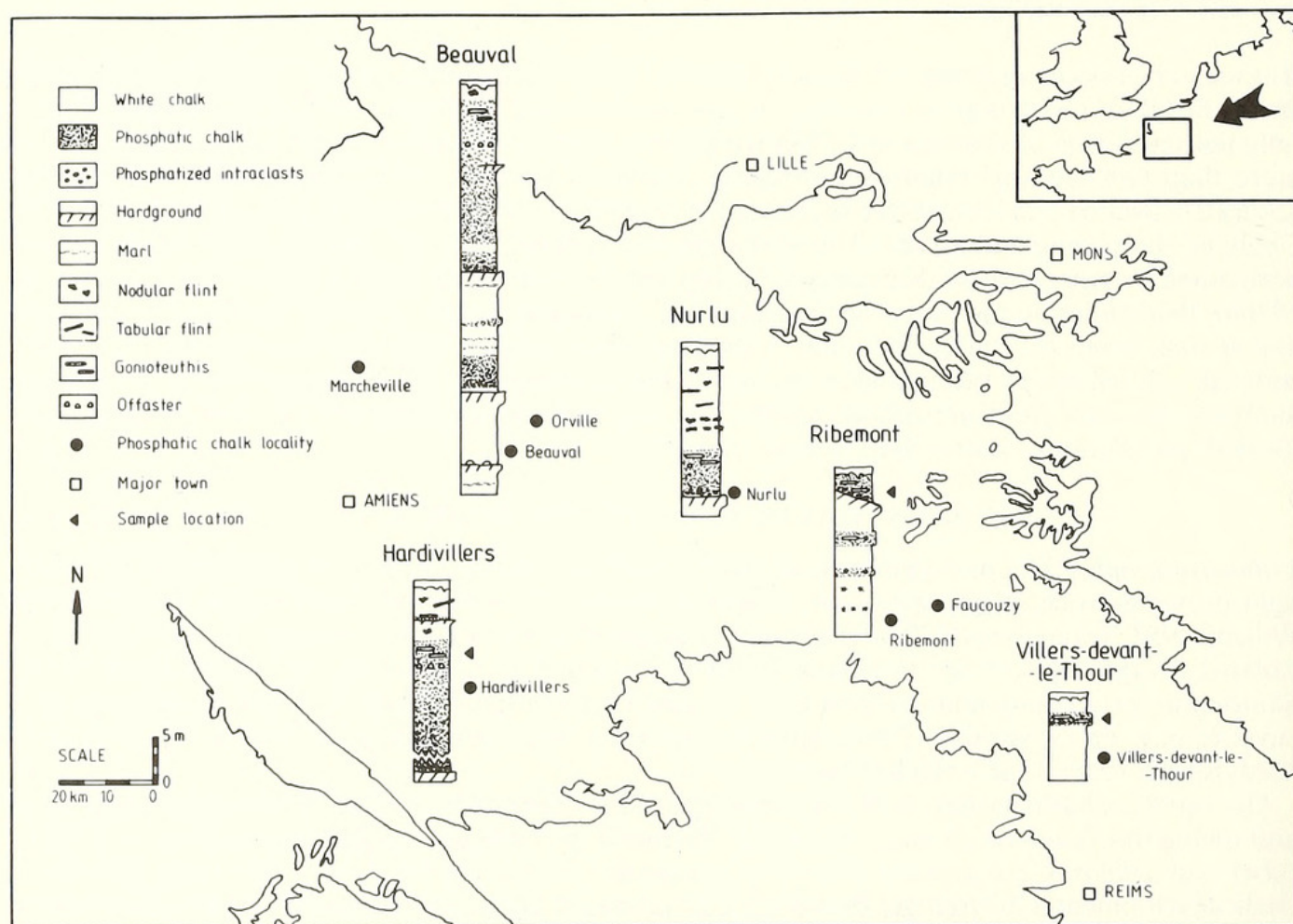
Lithostratigraphy. The phosphatic chalks of Picardy in northern France are pelletal chalks rich in light-brown granules of phosphatized carbonate, many of which are of faecal origin (Cayeux 1939; Willcox 1953; Tabataba'i 1977), and contain in excess of 5% P_2O_5 . They occur in small groups of, or isolated troughs up to 1 km in length, 250 m wide and 30 m deep in the soft white chalks of the Santonian-early Campanian of northern France and southern England. These troughs, termed *cuvettes* (e.g. de Grossouvre 1901), have an erosional origin and are floored by a well-developed hardground, termed the basal hardground.

On top of the basal hardground there rests up to 15 m of phosphatic chalk which contains a prolific and distinctive fauna at its base, including '*Terebella*' *phosphatica* Leriche (an agglutinated worm tube) and *Diblasus arborescens* Parent (a compound coral) (Jarvis 1980). The final phosphatic chalk development is no younger than early Campanian in age and usually contains distinctive bands of *Offaster pilula* Lamarck and *G. quadrata quadrata* (Blainville). The genesis of these deposits is discussed elsewhere (Jarvis 1980). Despite the relative abundance of fauna at certain levels within phosphatic chalks, little information has been published on their macrofauna, although short faunal

lists and descriptions are provided by Leriche (1908, 1911). The common occurrence of *G. ex gr. quadrata* in the upper portion of phosphatic chalks has been noted previously by several authors (Lasne 1902; Gosselet 1901; de Grossouvre 1894, 1899, 1901, 1907; Leriche 1908, 1911; Jarvis 1980).

A large 'population' of over 200 guards was collected by the author in 1977–1978 from the abandoned phosphorite quarry near Hardivillers (Oise). A further 100 guards were collected from Ribemont (Aisne) and Villers-devant-le-Thour (Ardennes) quarries, together with additional comparative material from several other phosphatic chalk localities. All of the material utilized in the present study (deposited in the Oxford University Museum—OUM) was collected, where possible, *in situ* and carefully localized by reference to the lithostratigraphy. The location [Lambert coordinates provide an east-west (x) and north-south (y) position (± 50 m) on a standard map-grid, plus the height (z) above sea-level (± 5 m)] and lithostratigraphy (text-fig. 1) of the three quarries is described briefly, and in addition details are provided for Beauval quarry (Somme), since this provides the most complete extant example of the phosphatic chalk lithofacies, and is the source of much of the comparative material.

Hardivillers quarry (Oise) x 593,22 y 213,74 z 120. A large complex of abandoned quarries lying 1.5 km north-east of the village of Hardivillers, north of the N30 between Hardivillers and Breteuil. Although mentioned by a number of authors (Buteux 1849; Lasne 1890, 1892; de Mercey 1887; Meunier 1891; de Grossouvre 1901, 1907; Tabatabaï 1977), little has been published on the succession. The quarries expose a 4–12-m-thick bed of phosphatic chalk resting on top of a strongly indurated and mineralized basal hardground. The succession may be divided conveniently into three units: a lower white chalk, a phosphatic chalk, and an upper white chalk. Two



TEXT-FIG. 1. Location and lithostratigraphy of phosphatic chalk localities referred to in the text. The solid lines are the limit of the Upper Cretaceous outcrop.

major biostratigraphical marker horizons are present within the phosphatic chalk: a lower 30-cm bed of abundant *O. pilula*, termed the Hardivillers Offaster Bed, and an upper 1-m-thick bed with abundant *G. q. quadrata*, termed the Hardivillers Gonioteuthis Bed. The bulk of material considered in this paper originates from the latter bed which yielded 270 specimens (OUM KZ6001–KZ6270), of which 136 were complete guards.

Ribemont quarry (Aisne) x 193,47 y 340,63 z 90. A small, intermittently worked quarry, 2 km south-east of Ribemont village. The quarry is situated off the minor road leading to 'la Ferme à Chaux', south of the D12 which links Ribemont to Villers-le-Sec. The site was described by Rabelle (1893, 1902) who noted the abundance of *G. ex gr. quadrata* in the upper part of the section. The locality has never been worked for phosphorite but exposes three thin beds of phosphatic chalk intercalated within the soft, white, flintless chalk which forms the bulk of the sequence. The 'population', which originates from the uppermost phosphatic chalk, consists of 174 specimens (OUM KZ6281–KZ6455), of which seventy-three are near-complete guards. The sediment log (text-fig. 1) illustrates the considerable relief (up to 1.5 m) on the Ribemont Gonioteuthis Hardground, a strongly lithified and mineralized hardground which underlies the uppermost phosphatic chalk. The hardground has a bow-shaped cross-section in the central upper portion of the quarry face, which is interpreted as a synsedimentary depression in the surface of the hardground.

Villers-devant-le-Thour quarry (Ardennes) x 725,35 y 201,50 z 100. An intermittently worked quarry 1.5 km west-south-west of Villers-devant-le-Thour, on the south side of the D18 which joins the village to the N366. The locality is referred to by de Grossouvre (1901, p. 126), Broquet (1973), and Guérin, Maucorps, Solau, and Pomerol (1977) but no details are given. The exposure consists of 8.5 m of soft white chalk (text-fig. 1), which includes a 1-m-thick bed of phosphatic chalk towards its top. The phosphatic chalk contains abundant oyster and fish debris, frequent pectinids, and *Gonioteuthis*. The bed cuts down and thickens to nearly 2 m towards the eastern side of the quarry. Here, at its base, a 50-cm unit of large (up to 10 cm) phosphatized intraclasts and abundant *G. ex gr. quadrata* provides the source of the sixty nine guards (OUM KZ6480–KZ6549), including twenty four near-complete examples, analysed in this paper.

Beauval quarry (Somme) x 599,89 y 266,80 z 130. A large quarry on the east side of the N16, 6 km due south of Doullens and on the east side of Beauval village. Beauval is probably the best documented of all phosphatic chalk localities (Buteux 1849; Meunier 1888; de Mercey 1890; Lasne 1890, 1892, 1902; de Grossouvre 1901; Briquet 1902; Negre 1912, 1963; Tabatabaï 1977; Jarvis 1980) but despite the wealth of literature, little stratigraphical information is available, except for Tabatabaï's (1977) foraminiferal zonation. The site displays two major levels of phosphatic chalk (text-fig. 1) both resting on top of well-developed hardgrounds. The upper phosphatic chalk contains the Beauval Offaster Bed and Beauval Gonioteuthis Bed, similar to those seen at Hardivillers, towards its top. Specimens of *Gonioteuthis* have been collected from throughout the sequence, but are scarce except in the phosphatic chalk which directly overlies the upper basal hardground and the Beauval Gonioteuthis Bed itself. Insufficient well-preserved material was available for statistical analysis, but the site provides important comparative material.

Other sites. Three other specimens are included in the comparative diagrams. One (KZ6601) originates from a minor phosphatic chalk intercalated within the upper white chalk at Faucouzy quarry (Aisne) (x 691,75 y 233,63 z 129). The other two (KZ6788, KZ6801) come from the phosphatic chalk which directly overlies the basal hardground at Nurlu quarry (Somme) (x 647,65 y 254,60 z 140).

Belemnite biostratigraphy. Four genera of belemnite occur in the Santonian–early Campanian deposits of the Anglo-Paris Basin. These are *Actinocamax* Miller, 1829, *Belemnelloamax* Naidin, 1964, *Gonioteuthis* Bayle, 1879, and *Belemnitella* d'Orbigny, 1840. Of the four genera, *Belemnitella* is restricted to one species (*B. praecursor* Stolley), *Belemnelloamax* to one group (*B. ex gr. grossouvrei* (Janet)), and *Actinocamax* also to one species (*A. verus* Miller). The genus *Gonioteuthis*, on the other hand, is represented by an evolutionary lineage of six species and is consequently the most stratigraphically useful of the four genera.

Gonioteuthis has been studied in detail by Stolley (1897, 1916, 1930), Ernst (1963a, b, 1964, 1966, 1968), Ernst and Schultz (1974), and Christensen (1971, 1973, 1975a, b). The genus includes the evolutionary lineage *G. westfalica* (Schlüter) (oldest), *G. westfalicagranulata* (Stolley), *G. granulata* (Blainville), *G. granulataquadrata* (Stolley), *G. quadrata quadrata* (Blainville), and *G. q. gracilis* (Stolley) (youngest), and is an outstanding example of phyletic gradualism (Christensen 1976b). The

Goniot euthis stock extended from the middle Coniacian to the top of the early Campanian, a period of some 10 million years (Van Hinte 1976). The genus shows three main trends during its evolution:

(1) Progressive calcification of the anterior portion of the guard, which evolves from a convexly conical, flat, or shallow alveolus in *G. westfalica* to a deep pseudoalveolus constituting up to one-third of the length of the guard in specimens of *G. q. quadrata*.

(2) The development of granulation, which is non-existent or poorly developed in specimens of *G. westfalica*, but is pronounced in *G. granulata* and stratigraphically younger species.

(3) Increasing size and stoutness of the guard, which reaches a maximum with *G. granulataquadrata* and early forms of *G. q. quadrata*.

G. westfalica is further isolated from the other species by its greater variation in guard shape and oval to pointed anterior cross-section, as compared to sub-rectangular to sub-quadrate in later species. The evolution of *G. q. gracilis* during the latest early Campanian marks a reversal of some of the general trends, with the return of slimmer, shorter guards and more shallow pseudoalveoli. The species does, however, remain distinct by the continued prominence of granulation and the presence of a notched pseudoalveolus (Ernst in Christensen 1975a, p. 37).

De Grossouvre (1894, 1899, 1901, 1907) suggested a threefold division of French phosphatic chalks based on his observations at Hardivillers. He dated the lowest phosphatic chalk at that locality as early Santonian (*Micraster coranguinum* Zone), a conclusion which is consistent with the foraminiferal evidence (Biozone e, Tabatabaï 1977). His lower unit was typified by *M. coranguinum* (Leske) and *A. verus*, the middle unit by *G. ex gr. quadrata* and *O. pilula*, and the upper unit by *G. ex gr. quadrata* and *B. 'mucronata'*. The overlying upper white chalk also contains the latter two species together with *M. pseudoglyphus* de Grossouvre (de Grossouvre *op. cit.*).

I have confirmed this general classification, with some additional details. *G. granulata* has previously been identified from a small number of localities (Leriche 1908) and certainly this belemnite is present in the lowest phosphatic chalk at Beauval and Nurlu; furthermore, fragments of *Goniot euthis* have been collected from a similar level at Hardivillers. De Grossouvre's record of *B. mucronata* (Schlotheim) is regarded as a misidentification of *B. praecursor* (Pl. 115, figs. 1–3, 9), which forms a minor element of the belemnite fauna in the Hardivillers *Goniot euthis* Bed (3%) and in the uppermost phosphatic chalk at Ribemont (4%).

A. verus (Pl. 115, figs. 10–13) is the commonest belemnite in the lowest phosphatic chalk at Beauval, Hardivillers, and Nurlu, but proportions and relative abundancies vary. At Nurlu fifty fragments and seven complete *A. verus* (KZ 6733–6738, KZ6763; Pl. 115, figs. 10, 11), and a well-preserved guard of *G. granulata* (KZ6788; Pl. 115, fig. 7) were collected from the lag on top of the basal hardground, yet at Beauval despite the larger fauna collected, no belemnites were found in the basal lag. In the lowest phosphatic chalk at Beauval, however, five specimens of *A. verus* (KZ6552–6556; Pl. 115, figs. 12, 13) and one *G. granulata* (KZ6551; Pl. 115, figs 4–6, 8) were recovered. *Belemnello camax ex gr. grossouvrei* has been described from phosphatic chalks (de Grossouvre 1894, 1899, 1901, 1907; Leriche 1908, 1911), but despite the collection of several hundred belemnites, no examples of this species were recovered by the author. De Grossouvre (*op. cit.*) suggests that this belemnite is typical of the lower portions of phosphatic chalks.

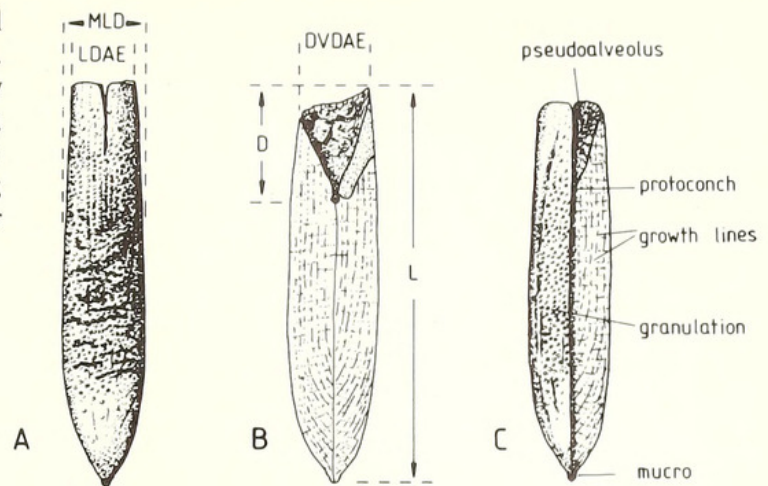
BIOMETRY OF *GONIO TEUTHIS* FROM PHOSPHATIC CHALKS

Statistical methods

The variation within belemnite 'populations' and their identification has been based on a series of univariate and bivariate statistics, histograms, and scattergrams similar to those applied by Christensen (1970, 1971, 1973, 1974, 1975a, 1976a) and Christensen, Ernst, Schmid, Schulz, and Wood (1975). Most statistical parameters were calculated utilizing an SPSS (Statistical Package for the Social Sciences) version 7 package on an ICL 2980 computer at the University of Oxford.

Guard morphology. The following characters (text-fig. 2) were measured: total length of guard (L), depth of the pseudoalveolus (D), dorso-ventral diameter at the alveolar end (DVDAE), lateral diameter at the alveolar end

TEXT-FIG. 2. Diagram showing the morphological elements of the *Gonioteuthis* guard. A, ventral view. B, left lateral view of a ground guard. C, cut-away dorsal view. MLD = maximum lateral diameter; LDAE = lateral diameter at the alveolar end; D = depth of the pseudoalveolus; L = length of guard; DVDAE = dorso-ventral diameter at the alveolar end.

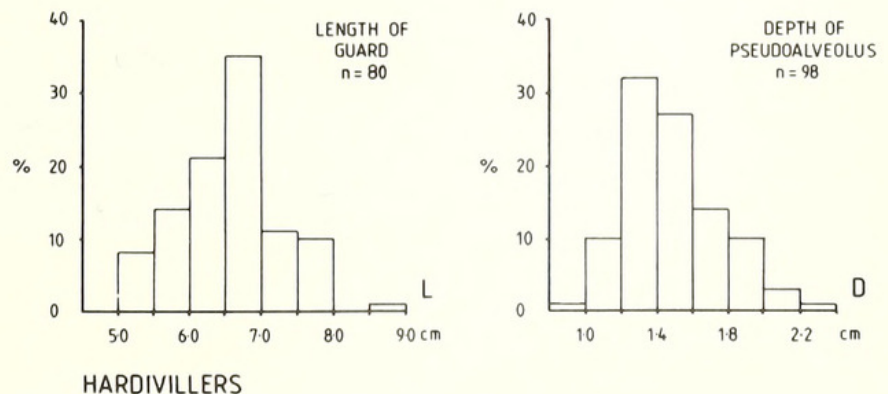


(LDAE), and maximum lateral diameter (MLD). Measurements were made with a vernier caliper to an accuracy of 0.1 mm. A number of other parameters, e.g. length of ventral fissure, have been measured by previous authors, but these have been found to be of little taxonomic value and have therefore been omitted. A small number of specimens were split to study the internal characteristics of the guard (method in Christensen 1971, p. 370), but since internal characters are of limited diagnostic use in the genus *Gonioteuthis*, no measurements were made on split material.

Univariate analysis. The following statistics were estimated: arithmetic mean (\bar{X}), standard deviation (SD), and coefficient of variation (CV). Histograms of two of the five characters (L, D) are shown in text-fig. 3. The frequency distributions were tested for normality using the Kolmogorov-Smirnov one sample test for goodness of fit. Clearly the univariate statistics of 'size' parameters can be effected by a large number of factors including sampling bias and *post-mortem* sorting; furthermore, a sample often contains an indeterminate number of juveniles (cf. Kermack 1954, p. 391) and in belemnites, as in Recent coleoids (Cousteau and Diol  1973, p. 93), there are no criteria for determining the ontogenetic stage of an individual (Christensen 1975a). Nevertheless, the values may be of interpretative value, although bivariate statistics are regarded as being of greater taxonomic significance.

Ratios. Ratios of 'size' parameters have been widely used in the study of belemnites. Ernst (1963a, b, 1964, 1966, 1968), in particular, characterized his samples of *Gonioteuthis* by mean values of various ratios, the most diagnostic of which were the Riedel-Quotient (ratio of length of guard to depth of pseudoalveolus) and the Schlankheits-Quotient (ratio of length of guard to dorso-ventral diameter at the alveolar end). Numerous authors (e.g. Shaw 1956; Simpson, Roe, and Lewontin 1960; Sokal 1965; Sokal and Rohlf 1969) have criticized the use of ratios. The main objections are that a ratio is a secondary statistic with greater variance than either of its components, that ratios may not be normally distributed, and lastly that if the relationship between the two characters is allometric, the ratio will change during growth. Despite these mathematical limitations, Ernst's *Gonioteuthis* stratigraphy based on mean Riedel-Quotient is generally valid, since the relationship between length of guard and depth of pseudoalveolus is isometric in nearly all samples of *Gonioteuthis* (Christensen 1975a, b), and furthermore the ratio has been found to be approximately normally distributed in the present study. Consequently, Riedel-Quotients (RQ) are reported for each sample.

TEXT-FIG. 3. Histograms of length of guard (L) and depth of pseudoalveolus (D) of *Gonioteuthis* from the Hardivillers *Gonioteuthis* Bed.



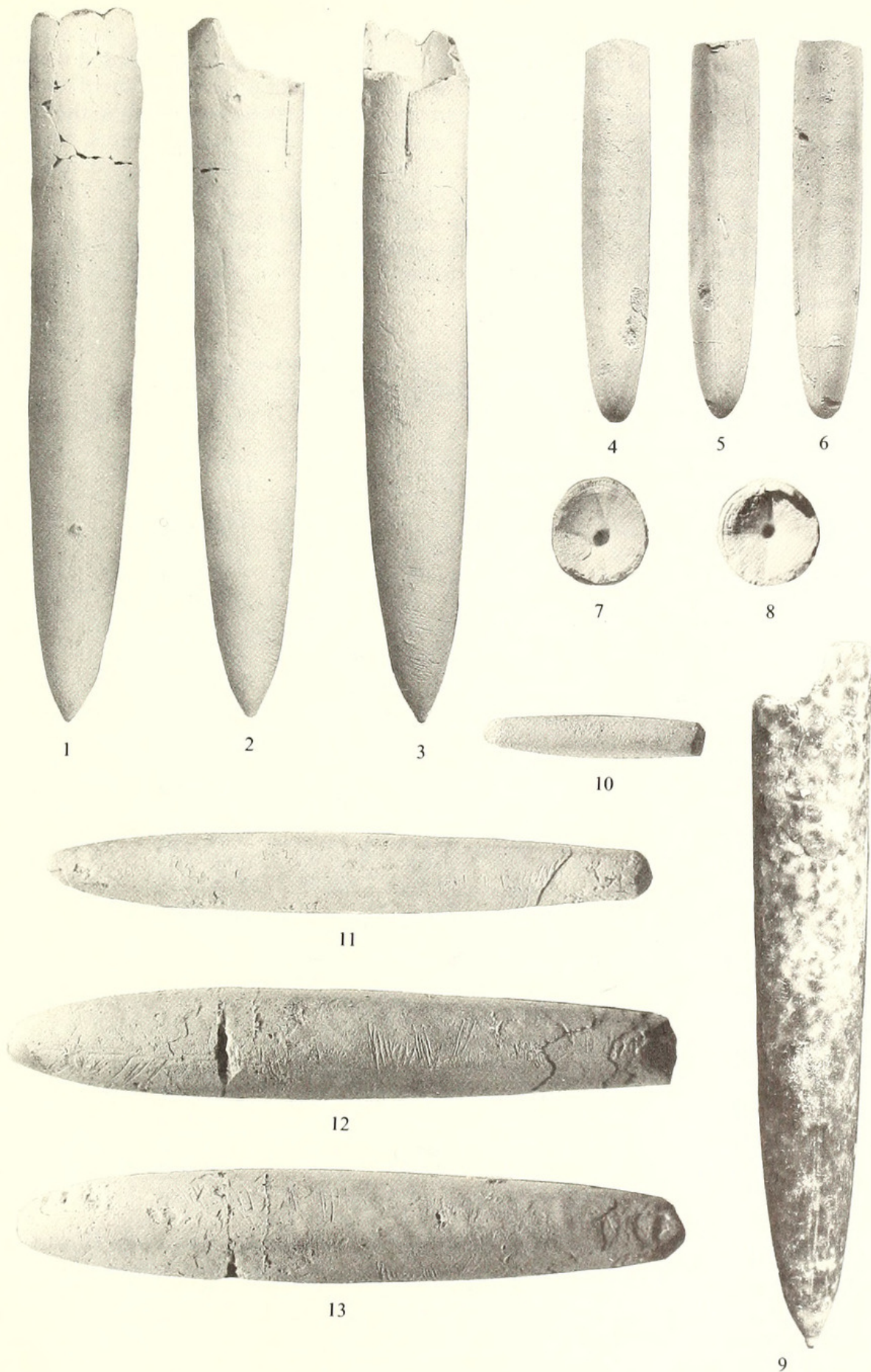
Bivariate analysis. The five 'size' parameters and the Riedel-Quotients were correlated utilizing Pearson Correlation Matrices. Regression analysis was used to study the relationship between variable pairs during growth. Regression lines were fitted by the least-squares method primarily because of the ability to compare the slope and intercept of different samples (see Christensen 1973, pp. 115, 116 for discussion). The regression line is written $y = a + bx$ and the original measurements were used because of their rectilinear trend on arithmetically scaled scatter-plots. The following statistical parameters were calculated: the percentage of variance explained by the linear relationship (r^2), the standard error of the y -intercept (SE_a), the standard error of the slope (SE_b), the standard error of the regression line (SE_{yx}), and the value of t (t_a), and the associated probability was calculated by t -testing the intercept on the y -axis to determine whether the intercept differed significantly from zero (Hald 1957). This final test has important biological implications since only a regression line passing through the origin represents isometric growth (i.e. $y = bx$). Other possible equations ($y = a + bx$; $y = bx^a$) represent allometric growth (the latter equation is often referred to as simple allometry, e.g. Christensen 1975a). The regression lines were compared with each other, and with comparable 'populations' from Germany, by the methods described by Hald (1957, pp. 571–579).

Results

The results of the univariate statistical analyses of the three 'populations' are given in Table 1. Although histograms of the various 'size' parameters show a slight asymmetry (text-fig. 3), statistical analysis utilizing the Kolmogorov-Smirnov one-sample test (Table 2) shows that all characters in all three 'populations' correspond well to a normal distribution. It was noted, however, that the probability associated with the length of guard for the Ribemont 'population' was considerably lower than that for the other two samples. Although no further specimens were available for detailed measurement, two parameters, length of guard and maximum lateral diameter, could be measured to a lower precision (± 0.25 and ± 0.05 cm respectively) on a further forty-three guards. The resulting histograms (text-fig. 4) are strongly bimodal, a K-S test giving D statistics of 0.1958 ($P = 0.03$) and 0.1891 ($P = 0.04$) respectively, both of which are significant at the 0.05 level. The mean length of the guards studied in detail from Ribemont is 6.30 cm, a value which lies in the trough between the two modes of the larger sample, indicating that the 'population' studied in detail is a mixture of two distinct components.

EXPLANATION OF PLATE 115

- Figs. 1–3. *Belemnitella praecursor* Stolley, from the Hardivillers Gonioteuthis Bed, early Campanian, *Offaster pilula* Zone. The anterior portion of the guard KZ6272 is missing. 1—dorsal, 2—left lateral, 3—ventral views, all $\times 1$.
- Figs. 4–6 *Gonioteuthis granulata* (Blainville). Lower phosphatic chalk, Beauval, early-middle Santonian, *Micraster coranguinum* Zone. The specimen is coated in a thin shiny phosphate patina, typical of basal lag preservation. Granulation is minimal. KZ6551. 4—dorsal, 5—left lateral, 6—ventral views, all $\times 1$.
- Fig. 7. *Gonioteuthis granulata* (Blainville). Base of phosphatic chalk, Nurlu, early-middle Santonian, *M. coranguinum* Zone. Anterior end of specimen KZ6788 with a pronounced rhombohedral anterior cross-section. Note the concentric growth rings, $\times 1.5$.
- Fig. 8. *Gonioteuthis granulata* (Blainville). Anterior view of KZ6551 (figs. 4–6). The guard has a circular cross-section. Note the shallow pseudoalveolus, $\times 1.5$.
- Fig. 9. *Belemnitella praecursor* Stolley. Uncoated right lateral view of KZ6272 (figs. 1–3). The specimen is honeycombed by *Entobia cretacea* Portlock, a clionid sponge boring. The fine (0.15–0.50 mm) surface pores can be seen in figs. 1–3, $\times 1$.
- Figs. 10–13. *Actinocamax verus* Miller. Base of phosphatic chalk, Nurlu (10, 11) and lower phosphatic chalk, Beauval (12, 13). Early-middle Santonian *M. coranguinum* Zone. 10, KZ6738, left lateral view of a juvenile guard, $\times 2$. 11, KZ6736, left lateral view of an adult guard, $\times 2$. 12, left lateral and 13, ventral views of a large specimen, KZ6556. Note surface wrinkling and tapering, pyramidal anterior termination to the guard, $\times 2$.



JARVIS, Cretaceous belemnites

All three samples, like *Gonioteuthis* 'populations' collected from other facies (e.g. Christensen 1974, p. 5; 1975, p. 32), are presumably an accumulation of several generations and consist of a growth series which both juveniles and adults (Pl. 116, figs. 1–15). The approximation of the length of guard size-distributions to normality results in mean length roughly corresponding to the size which most specimens had reached when they died. This is not true of the Ribemont sample, which shows two mortality peaks—around 5.0 and 6.8 cm. The second of these two maxima approximates to the mortality peaks of the 'populations' from Hardivillers and Villers-devant-le-Thour (Table 1) and from the early Campanian *O. pilula* Zone of south-west Münsterland (Ernst 1964, p. 126); material from Höver (Lower Saxony) (Ernst 1964, p. 132) has a lower mean length, approximately 6 cm, at this level. Comparisons with Ernst's results must be treated with caution, however, since he sorted out specimens of less than 4 cm length.

TABLE 1. Univariate analyses of the 'size' parameters of three 'populations' of *Gonioteuthis* from phosphatic chalks.

HARDIVILLERS

Character	N	\bar{X}	σ	CV	OR
<i>L</i>	80	6.537	0.701	10.72	5.00–8.67
<i>D</i>	98	1.475	0.257	17.42	0.93–2.26
DVDAE	94	1.032	0.158	15.31	0.71–1.45
LDAE	94	0.955	0.148	15.50	0.63–1.37
MLD	86	1.099	0.168	15.29	0.74–1.61
RQ	79	4.437	0.531	11.97	3.38–6.08

RIBEMONT

Character	N	\bar{X}	σ	CV	OR
<i>L</i>	12	6.303	0.678	10.76	5.43–7.21
<i>D</i>	10	1.608	0.322	20.02	1.15–2.11
DVDAE	5	1.162	0.134	11.53	1.05–1.38
LDAE	9	1.091	0.140	12.83	0.87–1.29
MLD	12	1.148	0.159	13.85	0.90–1.40
RQ	10	4.038	0.539	13.35	3.33–4.92

VILLERS-DEVANT-LE-THOUR

Character	N	\bar{X}	σ	CV	OR
<i>L</i>	8	6.749	0.603	8.93	5.94–7.62
<i>D</i>	10	1.649	0.300	18.19	1.23–2.05
DVDAE	9	1.256	0.196	15.61	0.91–1.52
LDAE	10	1.134	0.164	14.46	0.83–1.35
MLD	9	1.194	0.155	12.98	0.97–1.39
RQ	8	4.074	0.445	10.92	3.59–4.88

The smallest guard for which detailed measurements were obtained comes from Hardivillers and has an over-all length of 5 cm (Pl. 116, figs. 5–7); the smallest specimens from Ribemont lie within the range 3.5–4.0 cm. A number of guards with damaged pseudoalveoli and lengths of < 5 cm were also collected from Hardivillers, but the proportion of individuals within this size range is small. The rarity of small guards in most samples and the total absence of guards of less than 3.5 cm length may be attributed to the interaction of low juvenile mortality rate and high initial growth-rate. Such an interaction will also control the shape of the size-frequency distributions (Craig 1967; Surlyk 1972).

TABLE 2. Results of the Kolmogorov-Smirnov test for goodness of fit to a normal distribution for three 'populations' of *Gonioteuthis* from phosphatic chalks.

HARDIVILLERS

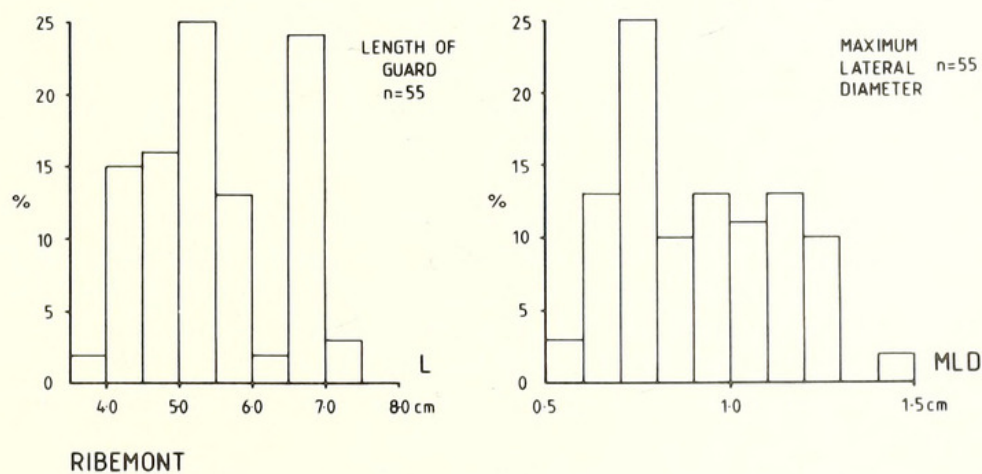
Character	N	D	Probability
L	80	0.0620	0.92
D	98	0.0783	0.59
DVDAE	94	0.0777	0.62
LDAE	94	0.0863	0.49
MLD	86	0.0559	0.95
RQ	79	0.1033	0.37

RIBEMONT

Character	N	D	Probability
L	12	0.2480	0.45
D	10	0.1384	0.99
DVDAE	5	0.2175	0.97
LDAE	9	0.1984	0.87
MLD	12	0.1075	1.00
RQ	10	0.1701	0.94

VILLERS-DEVANT-LE-THOUR

Character	N	D	Probability
L	8	0.1964	0.92
D	10	0.1324	1.00
DVDAE	9	0.1075	1.00
LDAE	10	0.0933	1.00
MLD	9	0.1395	1.00
RQ	8	0.2534	0.68

TEXT-FIG. 4. Histograms of length of guard (L) and maximum lateral diameter (MLD) of *Gonioteuthis* from the phosphatic chalk overlying the Ribemont *Gonioteuthis* Hardground.

The means of 'size' parameters of samples of *Goniatites* have been used successfully for the analysis of time trends in evolutionary lineages (Ernst 1964), and similar studies have been applied to *A. verus* (Reyment and Naidin 1962), but such studies are only viable with normally distributed characters. Since the mortality peak for early Campanian *Goniatites* is apparently between 6.5 and 6.8 cm length, the lower mortality peak of the Ribemont sample requires explanation. There are several possible interpretations which include:

- (1) the peaks represent different species;
- (2) 'size' parameter distributions are normally bimodal for 'populations' of *Goniatites*;
- (3) the 'population' has been current sorted or;
- (4) the bimodality is the result of a catastrophic event.

There is no morphological evidence to support the occurrence of more than one species of *Goniatites* within the Ribemont 'population'; however, stratigraphically close but specifically distinct *Goniatites* 'populations' would, once mixed, be impossible to separate on morphological criteria alone. No *Goniatites* 'population' has been described with a mean length as low as 5 cm and with appropriate mean Riedel-Quotient, but it should be noted that the value for *G. q. gracilis* from Misburg (Ernst 1964) does approach this value. Thus the possibility of specific mixing in the Ribemont phosphatic chalk cannot be totally dismissed although it is unlikely in my opinion.

Bimodality of 'size' parameters may result from annual or biannual mortality peaks of a species, but since no other 'populations' exhibit a bimodal distribution it must be concluded that such an explanation is invalid. Current sorting may lead to a reduction rather than an enhancement of the proportion of juveniles within a population, but transport of smaller individuals into the area of deposition remains a possibility. Bimodal distributions of this type frequently result from catastrophic events which cause the death of abnormally young 'populations', which are overprinted on the normal mortality curves. A storm deposit is the commonest example although Red-Tides provide a further possibility; the concentration of fauna into what is apparently a depression in the hardground accords most favourably with the storm-event hypothesis.

On the basis of univariate analysis the samples of *Goniatites* from Hardivillers and Villers-devant-le-Thour may be considered homogenous, while the 'population' from Ribemont is heterogenous. Consequently, interpretations made from the bivariate analysis of the small number of complete specimens available from this latter locality can only be regarded as tentative.

Ratios. In general, ratios have not been utilized in this study but the validity of the Riedel-Quotient is recognized (see above) as a method of species discrimination in specimens of *Goniatites*. Mean values of the Quotient for all three 'populations' (Table 1) lie within the range of values for *G. q. quadrata* (Ernst 1964, 1968), but individual specimens from Hardivillers (Pl. 156, figs. 1-15) may be referred to *G. granulata* (one specimen only), *G. granulataquadrata*, *G. q. quadrata*, or *G. q. gracilis*. Specimens from the other two localities may all be identified as either *G. granulataquadrata* or *G. q. quadrata* (or possibly *G. q. gracilis*). This range of possible 'species' within a single bed illustrates the importance of the study of 'populations' rather than individuals for the reliable identification of *Goniatites* species.

Regression analysis. All five 'size' parameters and the Riedel-Quotient were compared by means of Pearson correlation matrices (Table 3). The correlation coefficients for the Hardivillers 'population' were all highly significant ($P < 0.001$) except for the correlation between L and RQ which was less significant ($P < 0.03$). Probabilities associated with matrices from the other localities were generally higher, although all correlations remained significant at the 0.05 level in the Villers-devant-le-Thour sample, and only probabilities associated with RQ were not significant at this level for the Ribemont sample.

Since all five 'size' parameters are very closely related, four regression analyses were made for each 'population'. The plots chosen follow the usage of Christensen (1975a):

- (1) length of guard (x) versus depth of pseudoalveolus (y);
- (2) length of guard (x) versus dorso-ventral diameter at the alveolar end (y);

- (3) dorso-ventral diameter at the alveolar end (x) versus lateral diameter at the alveolar end (y);
 (4) maximum lateral diameter (x) versus lateral diameter at the alveolar end (y).

With three exceptions (Table 5) the relationships of the characters in the twelve analyses were isometric.

Length of guard (x) versus depth of pseudoalveolus (y). A regression analysis of these two characters provides an analogous but more comprehensive quantity than Ernst's Riedel-Quotient and is specifically the most diagnostic of the four regression analyses, partly because of the greater number of comparative analyses in the literature (e.g. Christensen 1971, 1973, 1975a). Christensen (1975a) has published regression analyses of Ernst's (1964, 1968) original measurements of six species of *Gonioteuthis*. The statistical parameters for these six 'populations' are given in Table 4 and the regression lines are plotted on the relevant scattergrams (text-figs. 5-7).

Hardivillers. The statistical parameters are given in Table 5 and the values plotted on text-fig. 5A. The 'population' was compared to *G. granulataquadrata* and was found to differ significantly in slope ($0.01 > P > 0.001$). A comparison with *G. q. quadrata* from the early Campanian *Inoceramus* ex gr. *lingua*-*G.* ex gr. *quadrata* Zone of Höver gave a highly significant correlation between slopes ($0.70 > P > 0.60$), but the position of the lines are different ($P < 0.001$). However, when compared with a stratigraphically younger 'population' of the same species (from the *Echinocorys conica*-*Galeola papillosa* Zone), the variances, slopes

TABLE 3. Pearson correlation matrices of the 'size' parameters of three 'populations' of *Gonioteuthis* from phosphatic chalks.

HARDIVILLERS

	L	D	DVDAE	LDAE	MLD	RQ
L	1.000	—	—	—	—	—
D	0.763	1.000	—	—	—	—
DVDAE	0.839	0.808	1.000	—	—	—
LDAE	0.825	0.810	0.980	1.000	—	—
MLD	0.814	0.711	0.955	0.940	1.000	—
RQ	-0.219	-0.786	-0.434	-0.426	-0.334	1.000

RIBEMONT

	L	D	DVDAE	LDAE	MLD	RQ
L	1.000	—	—	—	—	—
D	0.773	1.000	—	—	—	—
DVDAE	0.870	0.923	1.000	—	—	—
LDAE	0.817	0.785	0.985	1.000	—	—
MLD	0.800	0.631	0.992	0.952	1.000	—
RQ	-0.344	-0.850	-0.877	-0.530	-0.287	1.000

VILLERS-DEVANT-LE-THOUR

	L	D	DVDAE	LDAE	MLD	RQ
L	1.000	—	—	—	—	—
D	0.916	1.000	—	—	—	—
DVDAE	0.720	0.854	1.000	—	—	—
LDAE	0.794	0.900	0.970	1.000	—	—
MLD	0.916	0.900	0.946	0.959	1.000	—
RQ	-0.717	-0.931	-0.853	-0.943	-0.906	1.000

TABLE 4. Statistical relationship between depth of pseudoalveolus and length of guard for six species of *Goniatites* from Germany. $y = a + bx$ (modified from Christensen 1975a).

G. westfalica westfalica from the lower 'westfalica beds', Essen-Vogelheim (Ernst 1964a, p. 118; Christensen 1975a, p. 38)

$D = 0.1150 + 0.0597 L$; $N = 196$; $r = 0.2826$; $r^2 = 7.99\%$; $SE_a = 0.0828$; $SE_b = 0.0145$; $SE_{yx} = 0.1089$; $t_a = 1.3882$ ($0.20 > P > 0.10$)

G. westfalica granulata from Bülten (Ernst 1968, p. 278; Christensen 1975a, p. 38)

$D = 0.0102 + 0.1106 L$; $N = 51$; $r = 0.4809$; $r^2 = 23.13\%$; $SE_a = 0.1611$; $SE_b = 0.0279$; $SE_{yx} = 0.1146$; $t_a = 0.0633$ ($P > 0.90$)

G. granulata from Gleidingen (Ernst 1968, p. 278; Christensen 1975a, p. 38)

$D = 0.0701 + 0.1299 L$; $N = 45$; $r = 0.7311$; $r^2 = 53.45\%$; $SE_a = 0.0920$; $SE_b = 0.0185$; $SE_{yx} = 0.1083$; $t_a = 0.7620$ ($0.50 > P > 0.40$)

G. granulata quadrata from Weinberg (Ernst 1968, p. 278; Christensen 1975a, p. 38)

$D = 0.1030 + 0.1760 L$; $N = 45$; $r = 0.7404$; $r^2 = 54.82\%$; $SE_a = 0.1623$; $SE_b = 0.0244$; $SE_{yx} = 0.1370$; $t_a = 0.6342$ ($0.60 > P > 0.50$)

G. quadrata quadrata from the *I. ex gr. lingua*-*G. ex gr. quadrata* Zone of Höver (Ernst 1964a, p. 119; Christensen 1975a, p. 39)

$D = -0.0888 + 0.2685 L$; $N = 24$; $r = 0.7982$; $r^2 = 63.71\%$; $SE_a = 0.2640$; $SE_b = 0.0432$; $SE_{yx} = 0.2166$; $t_a = 0.3364$ ($0.80 > P > 0.70$)

G. quadrata quadrata from the *E. conica*-*G. papillosa* Zone of Höver (measurements by Ernst, statistics after W. K. Christensen, pers. comm.)

$D = -0.3776 + 0.2917 L$; $N = 65$; $r = 0.7649$; $r^2 = 58.51\%$; $SE_a = 0.1772$; $SE_b = 0.0309$; $SE_{yx} = 0.1711$; $t_a = 2.0977$ ($0.05 > P > 0.02$)

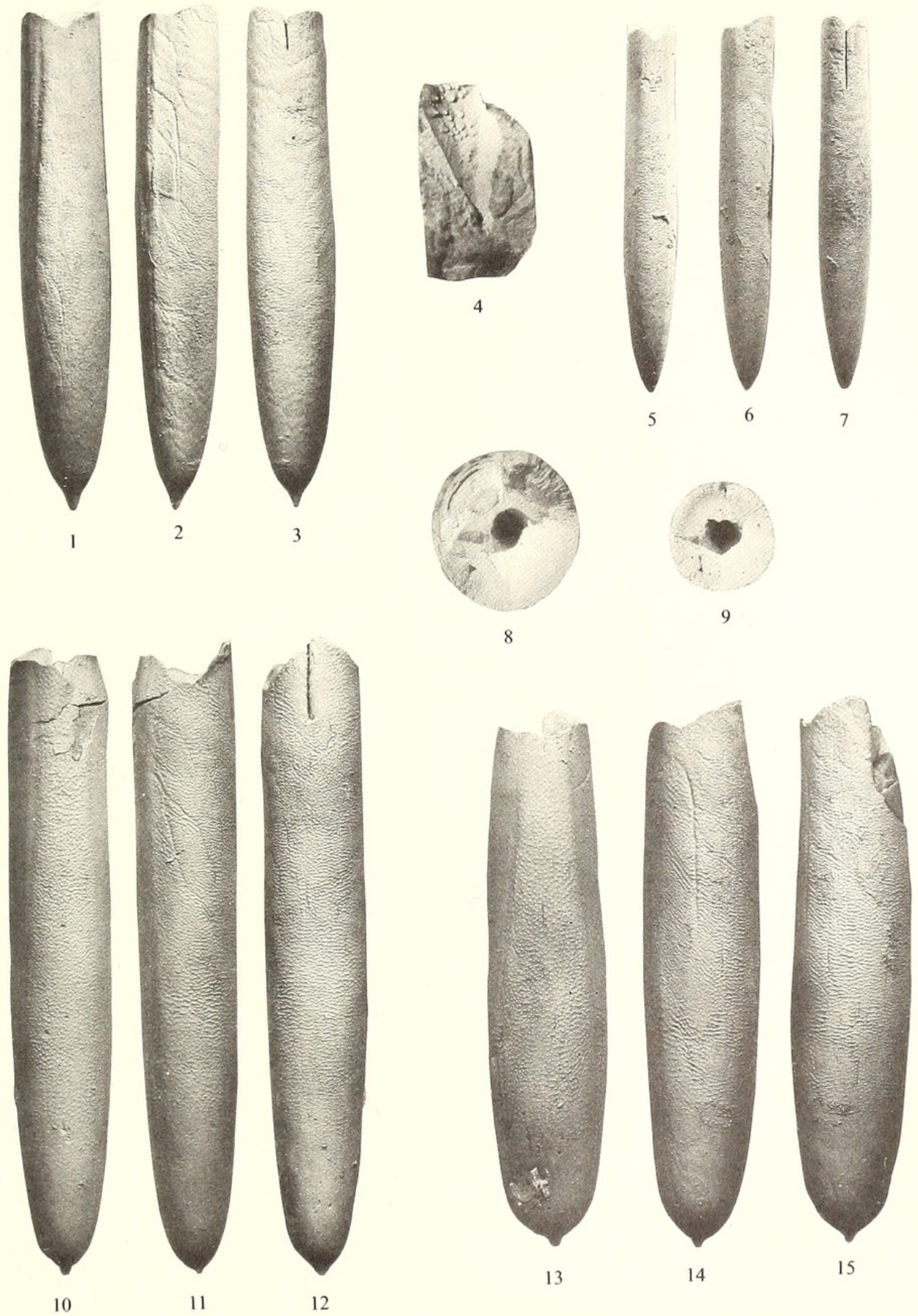
G. quadrata gracilis from the Germania IV quarry (north Germany) (Christensen 1975a, p. 42)

$D = -0.7641 + 0.3620 L$; $N = 47$; $r = -$; $r^2 = -$; $SE_a = 0.1820$; $SE_b = -0.0318$; $SE_{yx} = 0.1152$; $t_a = 4.1975$ ($P < 0.001$)

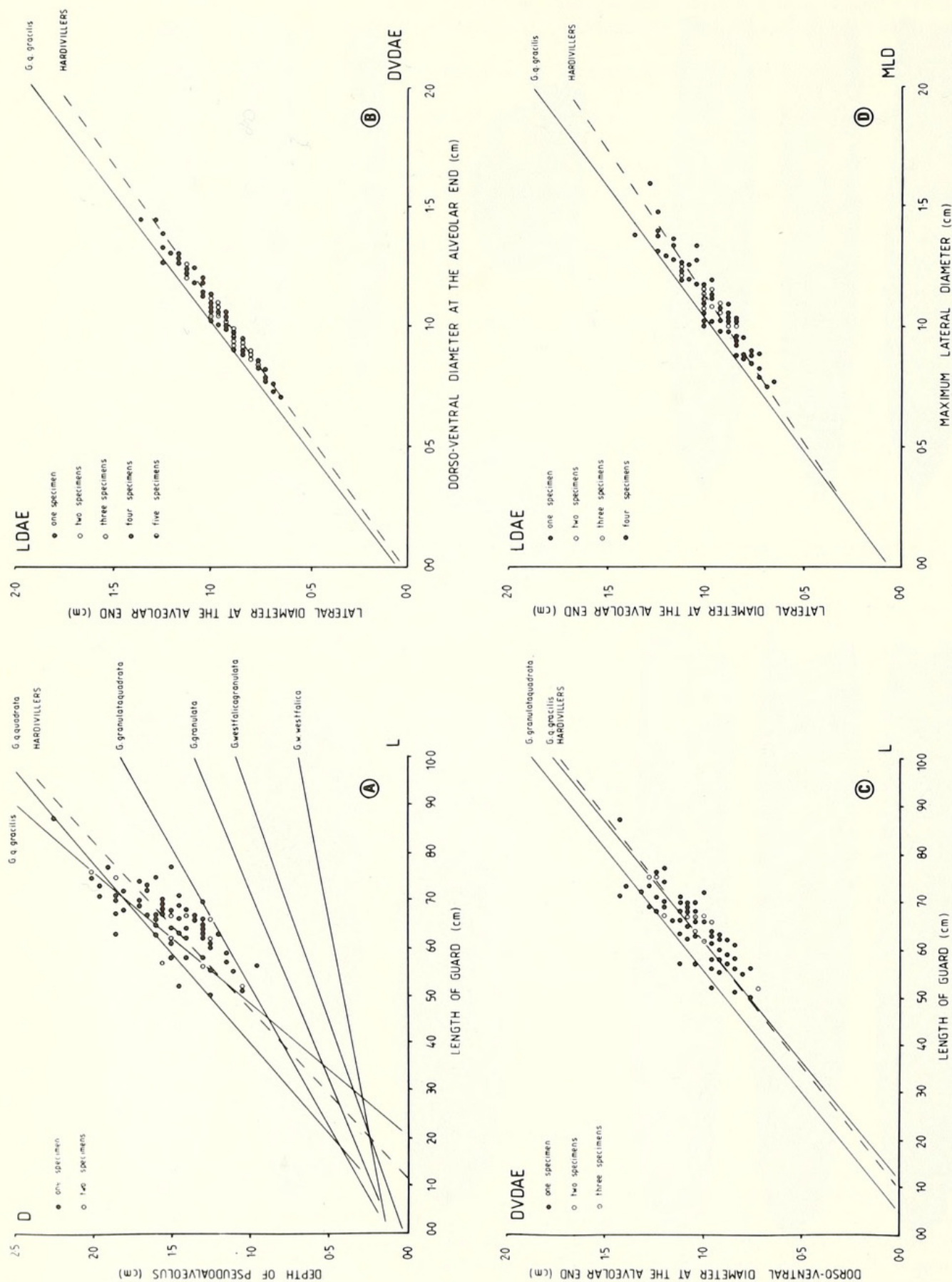
($P > 0.90$) and positions ($0.40 > P > 0.30$) of the lines were found to be the same, similar results were obtained from a comparison with a 'population' of *G. q. quadrata* from the 'Smectite' of Hallembaye quarry in eastern Belgium (W. K. Christensen, pers. comm.) where *G. q. quadrata* also occurs with *B. praecursor*. When compared to *G. q. gracilis*, the variances were found to differ significantly ($F = 2.2422$ with 77 and 45 degrees of freedom; $P = < 0.01$), so the test for non-equal variances was used (Hald 1957). The correspondence between the slopes of the two lines was found to be slightly significant ($0.10 > P > 0.05$ with 106 degrees of freedom) so the positions of the lines were also tested. The test gave a probability of $0.05 > P > 0.02$ with 122 degrees of freedom, which is not significant. Clearly the regression line compares most closely with that for *G. q. quadrata* from the Hallembaye 'Smectite' and the German *E. conica*-*G. papillosa* Zone. It is noteworthy that a *t*-test on the *y*-intercept for the younger *G. q. quadrata* 'population' from Germany, *G. q. quadrata* from Belgium, and the Hardivillers 'populations' gives significant values ($0.05 > P > 0.02$), indicating an allometric relationship between the characters as seen in *G. q. gracilis* (Christensen 1975a).

EXPLANATION OF PLATE 116

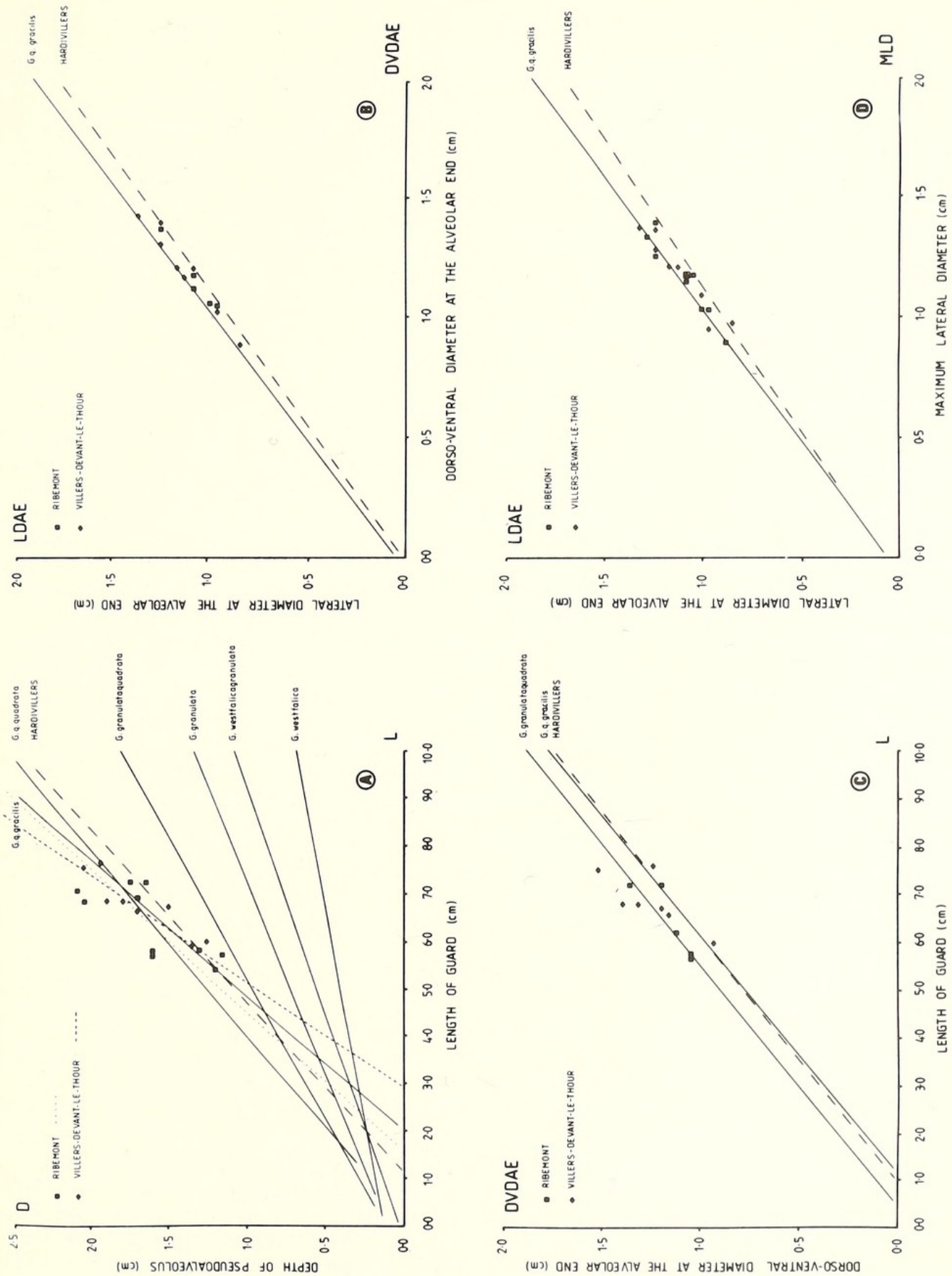
Figs. 1-15. *Goniatites quadrata quadrata* (Blainville) from the Hardivillers *Goniatites* Bed, early Campanian *Offaster pilula* Zone. 1-3, a medium-sized guard of average shape. KZ6040, dorsal, left lateral, and ventral views, $\times 1$. 4, split anterior end of KZ6099 showing conellae, $\times 1$. 5-7, an adolescent guard, KZ6033, the smallest complete specimen recovered from the bed, dorsal, left lateral, and ventral views, $\times 1$. 8, anterior end of KZ6066 (figs. 13-15) showing the depth of the pseudoalveolus, $\times 1.5$. 9, anterior end of KZ6040 (figs. 1-3) $\times 1.5$. 10-12, the largest specimen collected, KZ6039, dorsal, left lateral, and ventral views, $\times 1$. 13-15, the stoutest individual in the 'population', KZ6066, dorsal, left lateral, and ventral views, $\times 1$.



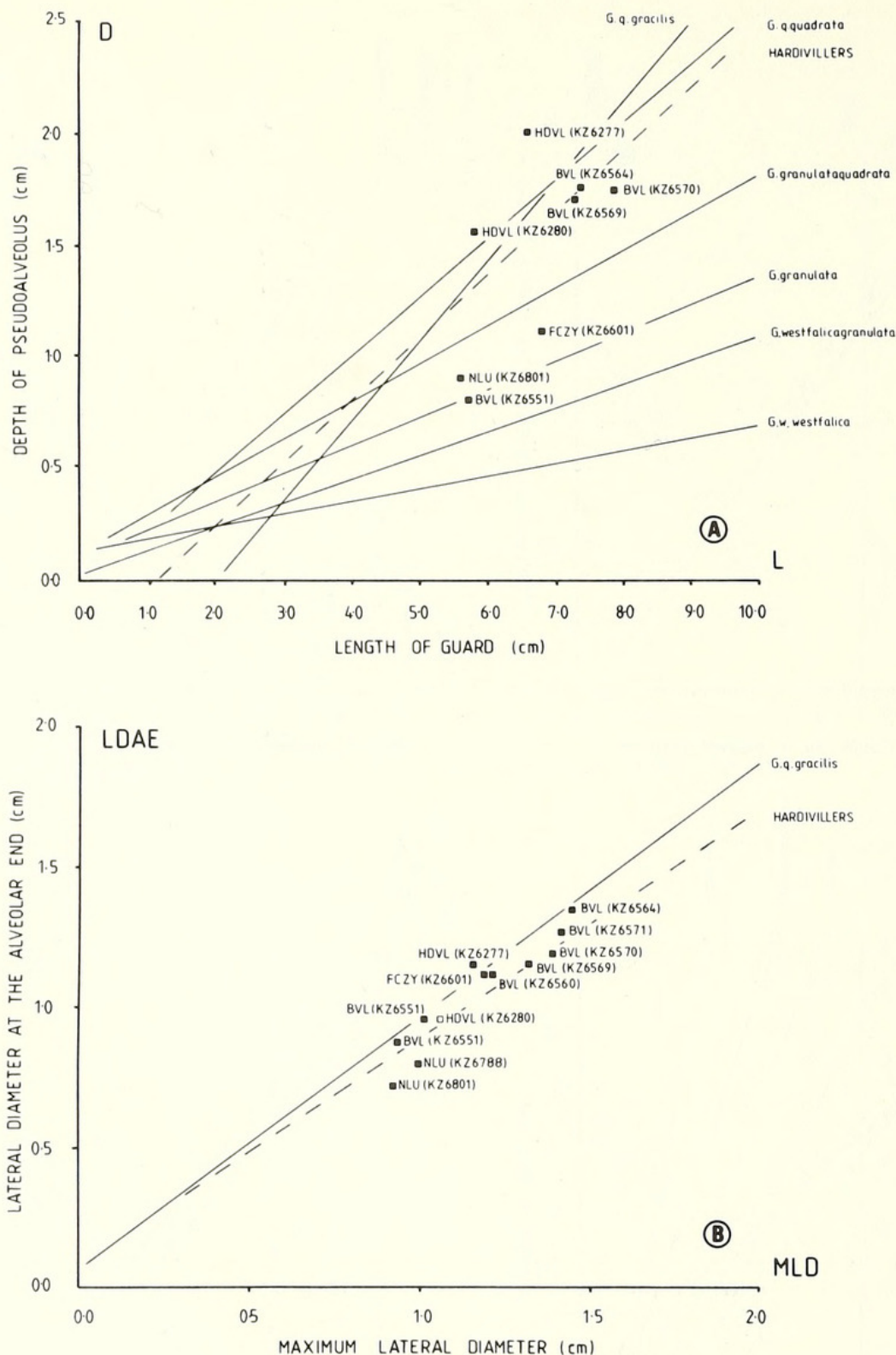
JARVIS, Cretaceous belemnites



TEXT-FIG. 5. Scatter diagrams and regression lines for *G. q. quadrata* from the Hardivillers Gonioteuthis Bed. A, length of guard (L) versus depth of pseudosulcus (D); the regression lines of six control 'populations' from Germany (Christensen 1975a) are plotted for comparison (the *G. q. quadrata* line is from the older Höver 'population'). B, dorso-ventral diameter at the alveolar end (DVDAE) versus lateral diameter at alveolar end (LDAE); the regression line for *G. q. gracilis* is plotted for comparison. C, length of guard (L) versus dorso-ventral diameter at the alveolar end (DVDAE); the regression lines of *G. q. quadrata* and *G. q. gracilis* are plotted for comparison. D, maximum lateral diameter (MLD) versus lateral diameter at the alveolar end (LDAE); the regression line of *G. q. gracilis* is plotted for comparison.



TEXT-FIG. 6. Scatter diagrams and regression lines for *G. ex gr. quadrata* from Ribemont and Villers-devant-le-Thour. The plots follow the same format as text-fig. 5.



TEXT-FIG. 7. Scatter diagrams of isolated specimens of *Gonioteuthis* collected from phosphatic chalks. A, length of guard (L) versus depth of the pseudoalveolus (D); the regression lines of the six German control 'populations' (excluding *G. q. quadrata* from the *E. conica*—*G. papillosa* Zone) and *G. q. quadrata* from Hardivillers are plotted for comparison. B, maximum lateral diameter (MLD) versus lateral diameter at the alveolar end (LDAE); the regression lines for *G. q. gracilis* from Germany and *G. q. quadrata* from Hardivillers are plotted for comparison.

Ribemont and Villers-devant-le-Thour. A comparison between the slopes and positions of the regression lines of the two 'populations' showed that they do not differ significantly ($P > 0.40$). A comparison between the slopes of the two lines and the slope of the Hardivillers 'population' also revealed no significant differences ($0.60 > P > 0.50$; $0.20 > P > 0.10$), but a comparison between the positions of the lines indicated that although the Ribemont belemnites differed significantly from those from Hardivillers ($0.01 > P > 0.001$), the Villers-devant-le-Thour and Hardivillers 'populations' are apparently the same ($0.10 > P > 0.05$). The two samples were compared to three species of *Gonioteuthis* from Germany (text-fig. 6A) and were found to differ significantly from *G. granulataquadrata*, but could correspond with either *G. q. quadrata* or *G. q. gracilis* both in slope and position. The small number of specimens available from these two localities makes the statistical data inconclusive. Certainly the 'populations' can be assigned to *G. ex gr. quadrata*, but subspecific identification remains uncertain. Intuitively the 'populations' correspond more closely to stratigraphically younger 'populations' of *Gonioteuthis* (text-fig. 6A) than that from Hardivillers (text-fig. 5A).

Analytical summary and comparisons

Individual specimens from all three localities have Riedel-Quotients within the range of values typical of *G. granulataquadrata* and *G. q. quadrata*, but the mean value for all three 'populations' is within the range of *G. q. quadrata*. The high degree of scatter of values of length of guard versus depth of pseudoalveolus has led to occasionally ambiguous results, but nevertheless the Hardivillers sample shows the greatest similarity to 'populations' of *G. q. quadrata* from the Hallembaye 'Smectite' and the *E. conica*-*G. papillosa* Zone of Germany. Unfortunately, no further 'size' parameter regression-analyses have been published for 'populations' of *G. q. quadrata* so it has been impossible to statistically compare other parameters with control 'populations'. However, unpublished data (W. K. Christensen pers. comm.) indicate that the Hardivillers sample may be distinguished from *E. conica*-*G. papillosa* Zone 'populations' on plots of L v. DVDAE. When this additional parameter is considered the Hardivillers sample is seen to be similar to a 'population' of *G. q. quadrata* from the *I. ex gr. lingua*-*G. ex gr. quadrata* Zone of Ziegelei Bremer, Bottrop-Fuhlenbrock (S. Münsterland) (Ernst 1964). Unfortunately, no regression data are available for this 'population' so a more precise comparison is impossible.

G. q. quadrata from Hardivillers can be distinguished from German 'populations' of *G. granulataquadrata* on L v. D and L v. DVDAE (text-fig. 5C) and from *G. q. gracilis* on L v. D and MLD v. LDAE (text-fig. 5D). It is noteworthy that the relationship between L v. D, L v. DVDAE and MLD v. LDAE must be considered allometric in the sample. The Ribemont and Villers-devant-le-Thour 'populations' cannot be distinguished from one another on any character or combination of characters. Generally the values lie closer to those of *G. q. gracilis* than to those of *G. q. quadrata* from Hardivillers. This is apparent in the plots of L v. D, DVDAE v. LDAE (text-fig. 6B) and MLD v. LDAE (text-fig. 6D), while in the plot of L v. DVDAE the values are closer to those of *G. granulataquadrata*. These observations demonstrate that the *G. ex gr. quadrata* from these two localities have a guard morphology similar to *G. q. gracilis* but are stouter than either German *G. q. gracilis* or *G. q. quadrata* from Hardivillers. It is suggested, therefore, that these 'populations' are stratigraphically younger than those from Hardivillers but are still *G. q. quadrata*, albeit more evolved forms.

Remaining complete specimens of *Gonioteuthis* which have been collected from phosphatic chalks are plotted on text-fig. 7. In the plot of D v. L (text-fig. 7A) three specimens clearly lie outside the scatter of values for the three 'populations' of *Gonioteuthis* from the facies (text-figs. 5A, 6A). All three specimens are identified as *G. granulata* on their Riedel-Quotients. Two of the three (KZ6551, Pl. 115, figs. 4-6, 8; KZ6801) come from the base of phosphatic chalk sequences, while the other (KZ6601) originates from above the main phosphatic chalk at Faucouzy. Material from Beauval (BVL) on the plot of D v. L comes from the upper portion of the upper phosphatic chalk and it all lies very close to the regression line for the Hardivillers 'population'. The additional examples from Hardivillers (HDVL) originate from the upper white chalk. It is noteworthy that both lie in the same region of the plot as the material from Ribemont and Villers-devant-le-Thour.

The plot of LDAE v. MLD (text-fig. 7B) shows a high degree of scatter between the two reference regression lines. All of the material from Beauval was collected from the upper phosphatic chalk

TABLE 5. Statistical results of regression analyses of four 'populations' of *Goniatites*.

HARDIVILLERS GONIOTEUTHIS BED

$y = a + bx$	N	r^2	SE_a	SE_b	SE_{yx}	t_a	Probability
D = $-0.3784 + 0.2870 L$	79	58.20%	0.1821	0.0277	0.1725	2.0775	$0.05 > P > 0.02$
DVDAE = $-0.1974 + 0.1933 L$	75	70.32%	0.0961	0.0147	0.0882	2.0538	$0.05 > P > 0.02$
LDAE = $0.0188 + 0.8978 DVDAE$	90	96.11%	0.0202	0.0193	0.0290	0.9331	$0.40 > P > 0.30$
LDAE = $0.0614 + 0.8264 MLD$	81	88.35%	0.0377	0.0338	0.0510	1.6316	$0.20 > P > 0.10$

PHOSPHATIC CHALK ABOVE THE RIBEMONT GONIOTEUTHIS HARDGROUND

$y = a + bx$	N	r^2	SE_a	SE_b	SE_{yx}	t_a	Probability
D = $-0.5653 + 0.3417 L$	10	59.76%	0.6343	0.0991	0.2166	0.8913	$0.40 > P > 0.30$
DVDAE = $0.1310 + 0.1604 L$	5	75.54%	0.3404	0.0527	0.0768	0.3849	$0.80 > P > 0.70$
LDAE = $0.1894 + 0.7665 DVDAE$	5	96.95%	0.0918	0.0786	0.0211	2.0629	$0.20 > P > 0.10$
LDAE = $0.0908 + 0.8526 MLD$	9	90.55%	0.1231	0.1041	0.0459	0.7376	$0.50 > P > 0.40$

PHOSPHATIC CHALK, VILLERS-DEVANT-LE-THOUR

$y = a + bx$	N	r^2	SE_a	SE_b	SE_{yx}	t_a	Probability
D = $-1.3240 + 0.4455 L$	8	83.90%	0.5396	0.0797	0.1271	2.4536	$0.05 > P > 0.02$
DVDAE = $-0.4975 + 0.2556 L$	7	51.88%	0.7578	0.1101	0.1476	0.6565	$0.60 > P > 0.50$
LDAE = $0.1007 + 0.8331 DVDAE$	9	94.01%	0.1009	0.0795	0.0440	0.9985	$0.40 > P > 0.30$
LDAE = $-0.0287 + 0.9533 MLD$	9	92.05%	0.1167	0.1059	0.0463	0.2459	$0.90 > P > 0.80$

G. q. gracilis, GERMANIA IV QUARRY, NORTHERN GERMANY (CHRISTENSEN 1975a)

$y = a + bx$	N	r^2	SE_a	SE_b	SE_{yx}	t_a	Probability
D = $-0.7641 + 0.3620 L$	47	—	0.1820	0.0318	0.1152	4.1975	$P < 0.001$
DVDAE = $-0.2428 + 0.2003 L$	47	—	0.0693	0.0121	0.0583	3.5054	$0.01 > P > 0.001$
LDAE = $0.0250 + 0.9064 DVDAE$	47	—	0.0253	0.0278	0.0290	0.9885	$0.40 > P > 0.30$
LDAE = $0.0506 + 0.9055 MLD$	47	—	0.0299	0.0339	0.0351	1.6910	$0.10 > P > 0.05$

except KZ6551 (Pl. 115, figs. 4–6, 8) which is from the base of the lower phosphatic chalk. The Hardivillers examples are from the upper white chalk. It is clear that the specimens from Nurlu (KZ6788, Pl. 115, fig. 7; KZ6801), which are both from the base of the phosphatic chalk, lie outside the scatter of values for the three 'populations'.

Scatterplots of DVDAE v. L and LDAE v. DVDAE do not have sufficient resolution to differentiate species of *Goniatites* on the small amount of comparative material available. These comparisons highlight the necessity for large collections in the identification of *Goniatites* species, but they also show that material from the base of phosphatic chalks may be attributed to *G. granulata* and that this species is readily distinguished on plots of LDAE v. MLD as well as Reidel-Quotient and D v. L plots.

Factor analysis

Since factor analysis requires listwise deletion of missing values, only the 'population' from Hardivillers was regarded as being of sufficient size to enable a statistically valid application of factor analysis. A total of sixty-nine guards were utilized in the analysis, results of which are given in Table 6.

The first principal component accounts for 87.2% of the variation and possesses a strong positive correlation with all of the 'size' parameters. It is interpreted as representing guard size, which is consistent with similar results from biological studies (Blackith and Reyment 1971, pp. 147–150) and for a 'population' of *A. plenus* from England (Christensen 1974). Clearly size is intimately related to age in marine invertebrates such as belemnites, although food availability may become an overriding factor in Recent coleoids (Mangold-Wirz 1963).

The second principal component accounts for 6.8% of the total variance. It shows a strong positive correlation with D, a moderate negative relationship with MLD, and negative correlations of approximately equal magnitude with DVDAE and LDAE. The factor is consequently interpreted as representing the evolutionary stage reached by each individual within the total 'population'. It reflects the increasing depth of the pseudoalveolus combined with a progressive increase in the slenderness of the guard from the maximum robustness reached in *G. granulataquadrata*.

The third principal component only allows for 4.6% of the observed variation. It shows a strong positive correlation with L and a weak negative interrelationship of approximately equal magnitude with the remaining characters. The factor may be interpreted as a shape effect which results in the production of elongate guards. Alternatively, it may be due to an indeterminate taphonomic control, perhaps sorting of material prior to deposition.

TABLE 6. Eigenvalues and Eigenvector matrix from a principal component factor analysis of *G. q. quadrata* from the Hardivillers Gonioteuthis Bed.

Eigenvector:	1	2	3
Eigenvalue:	4.361	0.342	0.228
Variance:			
% total	87.2	6.8	4.6
cumulative	87.2	94.0	98.6
Character			
L	0.902	0.043	0.429
D	0.860	0.492	−0.125
DVDAE	0.984	−0.099	−0.097
LDAE	0.974	−0.104	−0.116
MLD	0.943	−0.279	−0.077

Calculated from a 'population' of 69 guards.

TAPHONOMY AND DEPOSITIONAL ENVIRONMENT

Some degree of taphonomic bias will inevitably be present in any fossil assemblage. Consequently it is necessary to examine and if possible remove or 'allow for' any bias before zoological or stratigraphical conclusions can be reached. Furthermore, an assemblages' taphonomy, together with its associated sedimentology, may provide valuable insights into the depositional environment of that assemblage.

The majority of guards from the Hardivillers Gonioteuthis Bed are in excellent preservation and complete. A summary of the encrustation is given in Table 7. Although pycnodonteine oysters, octocorals, and serpulids are the major encrusters, a small number of cemented foraminiferids were present on some guards. Clionid sponge borings are present in many specimens (Pl. 115, figs. 1–3, 9) but they rarely form extensive networks. A second common form of boring consists of a radiating pattern of small (<0.1 mm) ramifying bores which occur just below the surface of the guards. These may be attributed to algae or fungi. Oysters are the dominant encruster (Pl. 116, fig. 13) but only 5% of specimens bear more than two individuals, and where larger numbers are present they are generally small and have identical orientations of their hinge-lines. Only four specimens exhibit more than a

single generation of encrustation, octocorals and serpulids following the pattern displayed by the oysters. The small size of the majority of the epifauna (oysters only reaching a few millimetres across) suggests that it is mostly juvenile. Examination of all specimens, including fragmentary guards, demonstrates that few, if any, show signs of mechanical abrasion, the poor preservation of the small number of broken guards being due predominately to the activities of boring sponges. Many belemnites display fine, subparallel scratch marks, (Pl. 115, figs. 12, 13; Pl. 116, fig. 13), generally oriented in a dorso-ventral direction and probably produced by the rasping action of a marine organism grazing the surface of the guards. Several guards show late-stage compactional effects, including partial crushing of their pseudoalveoli and *in situ* fracturing, occasionally accompanied by recementation of the dislocated fragments. Recent solution and partial decalcification, particularly in the area of the pseudoalveolus, has occurred in some material, but in general the guards are complete.

Specimens from the other localities display similar features to those seen in the Hardivillers sample. Most guards from Ribemont and Villers-devant-le-Thour are severely etched and corroded by weathering due to the proximity of the phosphatic chalk to the soil. Consequently, the data on the encrustation (Table 7) are less reliable for these sites. The guard from the basal lag at Nurlu (KZ6788), and hardground-associated guards from Faucouzy and Hallencourt display thin, shiny phosphate surface veneers (Pl. 115, figs. 4–6, 8) underlain by a portion of phosphatized calcite. In contrast to the opinion expressed by Tabataba'i (1977, p. 212), extensive phosphatization of belemnite guards was found to be uncommon.

TABLE 7. Summary of encrustation exhibited by three 'populations' of *Gonioteuthis* from phosphatic chalks.

Locality	Number of guards	Number encrusted (%)				
		Total	Oyster	Octocoral	Serpulid	> 1 species
Hardivillers	136	53	32	31	10	20
Ribemont	73	40	30	3	6	6
Villers-devant-le-Thour	24	6	6	0	0	0

The different proportions of encrusters and encrustation are not necessarily of environmental significance since they are too readily affected by the proximity of a 'spat' source. The well-preserved nature of the guards, the juvenile stage of the majority of the epifauna, and the lack of extensive boring suggest that burial was rapid. Furthermore, the general lack of more than one generation of encrustation indicates that re-exhumation was rare. These observations have important implications concerning the environment of deposition. The sedimentology indicates that the phosphatic chalk lithofacies was a relatively high-energy environment, within which the sediment was being winnowed by current action (Jarvis 1980). Yet the taphonomy of the belemnites suggests rapid burial and lack of re-exhumation. Clearly this removes the possibility of a low sedimentation rate due to continual winnowing as this would result in the belemnites being exposed on the sea floor for extended periods. Intermittent current action with rapid winnowing events followed by periods of quiescence and burial, therefore, seems a more likely mechanism. Such a cyclic process may also explain the apparent paradox between oxic bottom waters and sediment as demonstrated by the epi- and infauna and the subsurface anoxia associated with contemporary phosphorites (Baturin and Bezrukov 1979). It can be postulated that phosphatization took place during quiescent periods, and colonization and bioturbation during times of stronger current activity.

FACIES AND ECOLOGY

The abundance of belemnites within the phosphatic chalk lithofacies *vis-à-vis* soft white chalks requires some consideration. Both *Gonioteuthis* and *A. verus* occur very frequently in shallow-water deposits situated close to ancient massifs, such as the biocalcarenes and glauconitic sands of the Balto-Scandian area (Christensen 1976). Furthermore, *Gonioteuthis* from near-shore facies are characterized by the presence of all ontogenetic stages, while 'populations' from offshore chalks only contain adult specimens (Ernst 1964). This general trend also applies to other genera of belemnites, e.g. *Belemnitella* and *Belemnella*. It must be concluded that the occurrence of juveniles in phosphatic chalk 'populations' is indicative of a near-shore and therefore shallow-water environment for the facies.

In both facies belemnites are common just below, and particularly above, hardgrounds. The formation of Chalk hardgrounds is frequently accompanied by evidence of shallower-water conditions (Bromley 1965; Kennedy 1970; Kennedy and Garrison 1975; Jarvis 1980). This explains the occurrence of hardground associated belemnites in offshore chalks, but it does not explain their concentration in the phosphatic chalk environment which is initially also presumably shallow-water (Jarvis 1980).

It has been suggested (Surlyk and Birkelund 1977) that belemnites found in offshore chalks may be considered as straying adult individuals buried outside their normal habitat. Christensen (1976) has postulated that this apparent facies control may be causally related through the food-chain. Belemnites probably preyed upon small fish, crustaceans, and cephalopods, as do their Recent relatives (Naef 1922), and such prey would be more readily available in a shallow-water environment.

The association with hardgrounds results from the interaction of two independent factors. Firstly, hardgrounds are generally regarded as representing levels of faunal condensation whether due to omission (Kennedy and Garrison 1975) or active erosion coupled with winnowing (Jarvis 1980), or a combination of both processes. Either process would be expected to result in above-average concentrations of belemnites, but the taphonomy of the material indicates that the guards were not exposed on the sea floor for extended periods. The Ribemont sample, which originates from above a hardground, does have a greater proportion of bored fragments, but the proportion is considered insufficient to confirm the condensation hypothesis. Furthermore, the bimodality of the 'population' suggests deposition following a catastrophic event rather than long-term addition of material.

The second factor is the change in ecology which would be expected after sea-floor lithification. The new environment would embrace a mixed hard-soft substrate ecosystem, which might be expected to lead to an increase in diversity, and probably increased abundance of organisms. The increase in the sea-floor dependent biota would provide a food source for animals higher in the food chain, including the fish and crustaceans which are assumed to have been the main prey of belemnites. The two factors are not mutually exclusive and undoubtedly act in concert in the majority of cases, but I consider, on taphonomic grounds, that the second of the two factors predominates in phosphatic chalks.

The Recent coleoid *Loligo opalescens* generally inhabits water depths of 120–330 m but enters shallower water for mating and at night to feed. *L. opalescens* congregates in vast numbers to mate and reproduce, after which the majority of individuals die. An estimated 20 million dead have been observed on a small area off Baja California after such an event (Cousteau and Diolé 1973). Clearly this feature of the life cycle of a Recent coleoid, similar in size and morphology to the belemnites, provides one mechanism for the formation of the so-called 'Belemnitenschlachtfeld' (Belemnite battlefield) of the literature (e.g. Naef 1922).

The *Gonioteuthis* beds are around 1 m thick and contain belemnites scattered throughout, although patches of larger numbers of individuals occur. The higher concentrations are not at a particular level within the Beds nor are they on top of recognizable omission surfaces. It can be postulated, therefore, that these beds are the result of a series of mass mortalities following reproduction. The reproductive cycle of *L. opalescens* has another important aspect; after mating the squids attaches its eggs to epibenthic organisms and other suitable anchorage points on the sea floor (Cousteau and Diolé 1973; Recksiek 1978). It is suggested that hardgrounds would provide a greater

number of potential attachment sites than a soft substrate and would therefore be preferred as a breeding area.

It is not necessary to assume that the 'populations' of the *Gonioteuthis* beds were buried in the immediate area of their death. During the later stages of cuvette evolution, hardgrounds would be concentrated at the cuvette margins, where areas of lithified white chalk remained uncovered. These areas would provide preferred living/breeding sites for belemnites but, on death, individuals would be swept into the central portions of the cuvette and deposited. Subsequent bioturbation would remove the identity of individual mortality events and tend to disseminate guards throughout an interval of sediment. A further factor to be considered is the suggestion (Jarvis 1980) that phosphatic chalk formation was in part the result of upwelling of deep ocean water in the Anglo-Paris Basin, which provided the quantities of phosphate necessary for the deposition of such extensive phosphorites. Such an increase in orthophosphate would undoubtedly lead to higher plankton abundances which, as the base of the marine food-chain would result in increased numbers of higher animals including belemnites.

The *Gonioteuthis* beds occur at the top of the phosphatic chalks and perhaps represent an acme prior to the change in environment which resulted in the cessation of phosphatic chalk deposition. Such an acme might result from any of the factors discussed when considering the range of *A. verus* in phosphatic chalks (see below).

STRATIGRAPHICAL AND ENVIRONMENTAL CONTROLS

The facies model does not explain all aspects of the occurrence of belemnites in phosphatic chalks. The best-developed hardgrounds are at the base of phosphatic chalks, yet no basal hardground shows the concentration of *Gonioteuthis* guards typical of hardgrounds higher in the sequences. *A. verus* ranges from the Santonian to the early Campanian in Yorkshire (Jukes-Browne and Hill 1904; Wright and Wright 1942), Norfolk (Peake and Hancock 1961), and Germany (Schmid 1956; Ernst 1963a), but in southern England (Rowe 1901; Jukes-Browne and Hill 1904; Griffith and Brydone 1911) and northern France (de Grossouvre 1899) the species is apparently restricted to the Santonian, being particularly characteristic of the *Uintacrinus socialis* Zone. *Gonioteuthis*, on the other hand, appears infrequently in the Coniacian (as *G. westfalica*) chalks of northern France (de Grossouvre 1899, 1901, 1907) and southern England (Rowe 1901; de Grossouvre in Rowe 1901). Rare *G. westfalicagranulata* and *G. granulata* occur with *A. verus* in the mid-late Santonian of both areas (de Grossouvre 1899; Jukes-Browne and Hill 1904; Rowe 1904; Peake and Hancock 1961) but *G. granulata* is most abundant in the late Santonian *Marsupites testudinarius* Zone where *A. verus* is uncommon. The base of the early Campanian *Echinocorys depressula* Subzone of the *O. pilula* Zone is typified by forms intermediate between *G. granulata* and *G. q. quadrata*, i.e. *G. granulataquadrata* (Jukes-Browne and Hill 1904; Griffith and Brydone 1911), and *Belemnitella* (probably *B. praecursor*) makes its first appearance at this level (Jukes-Browne and Hill 1904). *G. q. quadrata* appears above the base of the Campanian in the 'Abundant *O. pilula*' Subzone of the *O. pilula* Zone and continues into the overlying *G. quadrata* Zone, where it becomes the index fossil (e.g. Griffith and Brydone 1911). Thus throughout the Anglo-Paris Basin *Gonioteuthis* is only relatively common in chalks where *A. verus* is rare or absent. This relationship is clearly shown by phosphatic chalks where the occurrence of the two genera is almost antipathetic. Explanations for this phenomenon must be sought from environmental, evolutionary, or provincial controls since it is not due to the relative ranges of the two fossils.

Firstly, the current regime which originally produced the cuvettes must have been of a higher order than that which accompanied their infill. This is demonstrated by the transition from erosion to deposition and may be reflected in the coarser and generally higher phosphate content of the lowest phosphatic chalks. In turn, changes in regime may be reflected in substrate and biota both within the cuvettes and elsewhere in the basin. Secondly, the major increase in the abundance of *Gonioteuthis* coincides with the evolution of *G. q. quadrata*. It might be suggested therefore that evolutionary changes in the *Gonioteuthis* stock may have enabled the genus to diversify and occupy previously

unfavourable niches. Broader environmental tolerances or changes in food requirements, for example, would provide a mechanism. Lastly, Jarvis (1980) has suggested that the initiation of phosphatic chalk sedimentation was in part due to major changes in oceanic circulation during the Santonian, which accompanied the opening of the Atlantic Ocean. Later changes in the distribution of water masses during the period of phosphatic chalk sedimentation may have enabled populations of *Gonioteuthis* to enter an area which, because of oceanographical conditions, was dominated previously by *A. verus* and *B. ex gr. grossouvrei*. Similarly, *A. verus* might have been excluded from that area. Any one, or a combination of these factors, can be invoked to explain the observed changes in belemnite distribution during the evolution of the lithofacies.

CONCLUSIONS

- (1) The phosphatic chalks of northern France provide rare examples of Santonian-early Campanian 'populations' of *Gonioteuthis*. This enables the application of statistical analysis in the identification of species.
- (2) These phosphatic chalks can be divided into three biostratigraphical subdivisions on their belemnite assemblages:
 - (a) a lower unit characterised by *A. verus* with *Micraster coranguinum*, occasional *G. granulata* and rare *B. ex gr. grossouvrei*;
 - (b) an intermediate division typified by *G. q. quadrata* with *O. pilula*;
 - (c) an upper unit with *G. q. quadrata* and occasional *B. praecursor*.
- (3) A combination of univariate and bivariate statistics demonstrates that the 'populations' from the Hardivillers *Gonioteuthis* Bed and the phosphatic chalk at Villers-devant-le-Thour are homogenous, whereas the 'population' from above the Ribemont *Gonioteuthis* Hardground is inhomogenous. Inhomogeneity in the latter sample is the result of a catastrophic event, probably a storm, which has resulted in the concentration of a mixed 'population' of young and old individuals.
- (4) Mean Riedel-Quotients for all three 'populations' fall within the range of *G. ex gr. quadrata* but subspecies cannot be identified on Riedel-Quotient alone.
- (5) *G. q. quadrata* has been identified as the subspecies present in the Hardivillers *Gonioteuthis* Bed. This 'population' of the subspecies shows an allometric relationship of L v. D, L v. DVDAE and MLD v. LDAE.
- (6) The Ribemont and Villers-devant-le-Thour 'populations' cannot be distinguished from each other but are distinct from that studied from Hardivillers. The subspecies at the former localities shows affinities to both *G. q. quadrata* and *G. q. gracilis*.
- (7) Principal component factor analysis illustrates that the major controls on *Gonioteuthis* guard morphology are:
 - (a) the size of the guard, which accounts for 87.2% of the observed variation;
 - (b) the evolutionary stage of the individual within the *Gonioteuthis* gradualistic series, 6.8% of the variation;
 - (c) a shape factor which produces elongate guards (or perhaps a taphonomic factor), 4.6%.
- (8) The well-preserved nature of the guards, the juvenile nature of the epifauna, and the absence of extensive boring suggest relatively rapid burial, while the general lack of more than one generation of epifauna implies that re-exhumation was rare.
- (9) Guard taphonomy suggests that the environment of deposition was one of intermittent current activity with rapid winnowing, followed by periods of quiescence and burial.
- (10) The occurrence of juveniles in the 'populations' indicates a shallow-water environment which was the belemnites' normal habitat because of the greater availability of food.
- (11) Belemnites are concentrated at hardground levels because of:
 - (a) a concentration of potential prey associated with the hardgrounds;
 - (b) the possibility that they may be preferred breeding sites and would therefore be the recipients of the large numbers of dead individuals following the mass mortalities which accompany reproduction.

- (12) The virtual mutually exclusive relationship between *A. verus* and *Goniot euthis* in phosphatic chalks may be controlled by:
- (a) the decline in the current regime during cuvette evolution favouring *Goniot euthis*;
 - (b) evolutionary changes in *Goniot euthis* allowing the genera to occupy a previously unfavourable niche and to oust *A. verus*, or
 - (c) changes in provincial boundaries which accompanied changes in oceanic circulation.

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