MORPHOMETRIC ANALYSIS OF *ACTINOCAMAX PLENUS* FROM ENGLAND

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A large sample of *Actinocamax plenus* (Blainville, 1825) from the Plenus Marls of the Betchworth Limeworks, Surrey, England, was studied by means of univariate, bivariate and multivariate statistical methods in order to analyse the variation. These studies indicate that three subspecies of *A. plenus,* viz.: *A. p. triangulus* Naidin, 1964, *A. p. longus* Naidin, 1964, *A. p. acutus* Naidin, 1964 and one subspecies of *A. primus* Arkhangelsky, 1912, viz.: *A. p. curtus* Naidin, 1964, cannot be consistently differentiated and therefore are synonymised. *A. plenus sinzowi* Nikitin, 1958 and *A. primus elongatus* Arkhangelsky, 1912 are also placed in synonymy because the evidence suggests that they are neither chronological nor geographical variants. The observed ranges of the length of the guard in *A. primus* and *A. plenus* are similar, whereas the modes of the same character in the two species apparently are dissimilar: c. 60–65 mm in *A. primus* and c. 75–80 mm in *A. plenus. A. primus* appears in the Lower Cenomanian and continues into the Middle Cenomanian whereas *A. plenus* in western and central Europe is confined to the *A. plenus* Zone of Late Cenomanian age. On the Russian Platform *A. plenus* starts in the late Upper Cenomanian and continues apparently into the Lower Turonian.

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The purposes of the present study are 1) to analyse the variation of a large sample (114 specimens) of *Actinocamax plenus* (Blainville, 1825) from England by means of univariate, bivariate, and multivariate statistical methods, and 2) to evaluate the mutual relationship of *A. primus* Arkhangelsky, 1912 and *A. plenus.*

A. plenus was established by Blainville (1825, p. 376) in the following statement: "Espèces droites, subtriquètres; la cavité très-petite et une fissure sur son bord, sans cloisons", but it was first figured two years later (Blainville, 1827a, pl. 11 bis, fig. 3). In the same year Blainville published another paper, "Mémoire sur les Bélemnites", which contained a more thorough description of *A. plenus,* and reported that the species is found in Kent, Sussex, and Wiltshire in England.

Sowerby (1829, p. 208, pl. 600, figs. 8 and 9) erected *Belemnites lanceolatus* as a distinct species but closely related to *A. plenus*. Sowerby stated that it has: "A much more elongated shell than B. plenus, which it much resembles; ...". According to Sowerby the specimens of *B. lanceolatus* were collected from Hamsey in Sussex.

The legitimacy of *B. lanceolatus* Sowerby has been extensively discussed in the literature. Sharpe (1853), Geinitz (1872–1875), and Schlüter (1874, 1876) considered *B. lanceolatus* Sowerby a junior synonym of *A. plenus,* whereas Jukes-Browne & Hill (1896, 1903, 1904), Grossouvre (1901–1903), and Stolley (1905, 1916) considered *B. lanceolatus* Sowerby a distinct species appearing earlier than *A. plenus* in the fossil record.

Because the species name *Belemnites lanceolatus* Sowerby, 1829 is a junior homonym of *Belemnites lanceolatus* Schlottheim, 1813, Jeletzky (1948, p. 339) replaced the junior homonym with the existing available name *Actinocamax primus,* which was erected by Arkhangelsky (1912) on specimens from the Russian Platform. Jeletzky designated as a lectotype the small specimen of *B. lanceolatus* Sowerby figured in Sowerby (1829), but unfortunately he stated fig. 8 on pl. 600 to be the type, which is the large specimen as pointed out by Birkelund (1957, p. 10). The smaller specimen reproduced as fig. 9 on pl. 600 is considered as the lectotype. Jeletzky (op. cit.) followed the view of Stolley and others that *A. primus* is a distinct species different from *A. plenus.* The same opinion has later been followed, inter alia, by Birkelund (1957), Naidin (1964), and Christensen (1970a, 1970b, 1973).

According to Arkhangelsky (1912) *A. primus* differs from *A. plenus* in being longitudinally striated and in possessing single lateral furrows. Naidin (1964) and Christensen (1973) have shown that this differentiation in not practical. According to Jeletzky (1948) *A. primus* differs from *A. plenus* in being smaller, more slender, not swollen posteriorly and has a centrally placed apical point. Birkelund (1957), however, showed that in the specimens of *A. primus* from the Arnager Greensand of Bornholm (Denmark) the apex is slightly displaced towards the dorsal side.

Provenance of the material

The material of *A. plenus* for this study was collected by Mr. G. W. Butler from the Plenus Marls in the Betchworth Limeworks and was obtained on loan from the Institute of Geological Sciences, London, (specimen numbers prefixed with Zb) and from the Sedgwick Museum, Cambridge, (specimen numbers prefixed with B). The locality is discussed in Dines & Edmunds (1933, pp. 99–100) and Kennedy (1969, p. 491).

Jefferies (1961, text-fig. 2) showed that *A. plenus* is confined to his beds 4–6 of the Plenus Marls in the Anglo-Paris Basin. The Betchworth Limeworks was not discussed by Jefferies, but according to Dines & Edmunds (1933) the thickness of the Plenus Marls in the Betchworth Limeworks is about 3 m (about 10ft.). At Merstham, the type locality of the Plenus Marls (Jefferies, 1963), which is situated about 6 km E of the Betchworth Limeworks, the thickness of beds 4–6 is about 30 cm. The age of the *A. plenus* Zone is discussed in the stratigraphic section below.

Methods of study

The following characters were measured: length of the guard (L), the dorso-ventral diameter at the alveolar fracture (DVDAF), the lateral diameter at the same place (LDAF), and the maximal lateral diameter (MLD) (cf. fig. 1). The measurements were made with a vernier caliper to an accuracy of 0.1 mm. This study includes only those specimens on which it was possible to measure all four characters. The collection contains an additional 24 specimens.

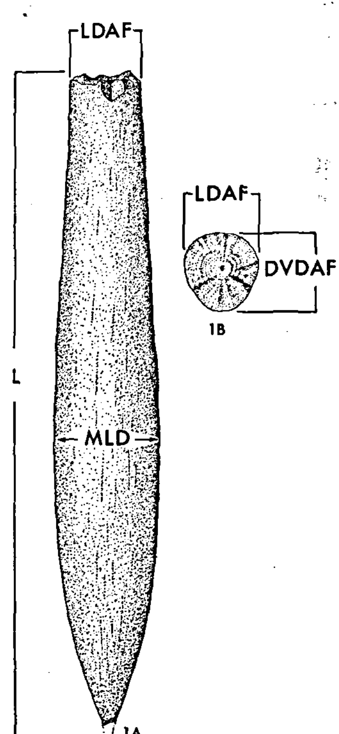


Fig. 1. The position of the measured characters with respect to the guard. A: Dorsal view. B: View of the adoral part of the guard. L = total length of the guard; MLD = maximal lateral diameter; DVDAF = dorso-ventral diameter at the alveolar fracture; LDAF = lateral diameter at the alveolar fracture.

In about 35 % of the specimens the outermost apical part of the guard was broken of. In these specimens the total length of the guard was estimated by adding 1–5 mm to the preserved part of the guard. The added values constitute less than 10 % of the total length of the guard.

Systematic description

Actinocamax plenus (Blainville, 1825)

Pl. 1, figs. 1–3; Pl. 2, figs. 1–5;
Pl. 3, figs. 1–6; Pl. 4, figs. 1–5.

For synonymy see p. 11.

General description

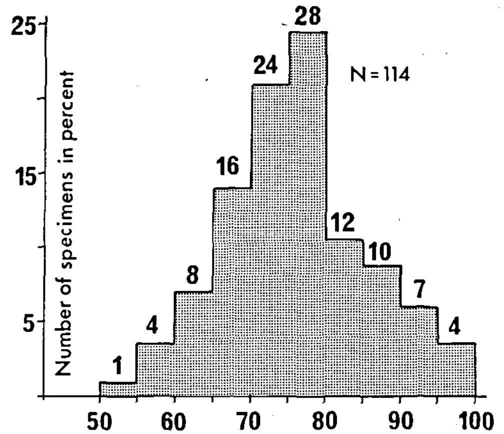
The guard in the present sample reaches a length of 98 mm, the mean value being 76 mm. The shape of the guard is variable due to the allometric growth relationships (cf. discussion below). Juvenile guards are subcylindrical to slightly lanceolate in ventral view, and subcylindrical in lateral view. The apex in juvenile specimens is only slightly or not at all displaced towards the dorsal side. Adult specimens are lanceolate or strongly lanceolate in ventral view, and subcylindrical or slightly lanceolate in lateral view. In these specimens the apex is displaced towards the dorsal side. The guard is flattened ventrally along its entire length and is compressed laterally in the adoral part.

The calcification of the adoral part of the guard is variable and results in specimens showing a shallow pseudoalveolus (about 7 % of the total sample of 138 specimens), but most specimens have a low cone-shaped alveolar fracture with a small pit in its center. However, the sample exhibits all intermediate forms. The alveolar fracture is asymmetric, the dorsal side being more incised than the ventral one, and the fracture is sharply demarcated from the surface of the guard. The cross-section of the adoral part of the guard is subtriangular or pointed oval with the dorso-ventral diameter exceeding the lateral diameter in most specimens. The alveolar cone exhibits the concentric growth layers of the guard and has radiating ribs. A dorsal embayment on the alveolar cone and a short ventral furrow may be present.

Dorso-lateral depressions are fully developed and the guard may be provided with a longitudinal striation and single lateral furrows.

In juvenile guards the apical part of the guard is very acute and these specimens do not have a well-defined mucro. In adult specimens the apical angle is less acute and a mucro is present.

Fig. 2. Histogram of the length of the guard in mm of *A. plenus* from the Betchworth Limeworks. The figures above the bars are the actual number of specimens.



Univariate analysis (N = 114)

Character	$\overline{X}$	SD	CV	OR
1. L	76.16	9.621	12.63	52.2–98.0
2. DVDAF	7.92	1.667	21.05	3.7–12.3
3. LDAF	7.46	1.520	20.38	3.5–11.5
4. MLD	10.27	2.256	21.97	4.3–15.9

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

A histogram of the length of the guard is shown in fig. 2. The histogram was tested for normality by the χ^2 test, and the test gave a value of 6.26 with 7 degrees of freedom, which is not significant ($0.70 > P > 0.50$). Histograms were also drawn for the three other characters. The three histograms show good approximations to the normal distribution and χ^2-tests were consequently not performed.

The sample of *A. plenus,* presumably an accumulation of several generations, consists of a growth-series probably containing both juvenile and adult specimens. Specimens with guards less than 52.2 mm in length naturally have existed, and the absence of these guards in the sample may be due to the extreme fragility of the thin and elongated juvenile guard (cf. fig. 3), which renders it very difficult to collect complete juvenile guards. Furthermore, the absence of small guards may be due to the interaction of low mortality-rate and high initial growth-rate of the juvenile specimens. Specimens of *A. plenus* and *A. primus* with a length of the guard less than c. 50 mm are infrequently reported in the literature (see figs 3, 6, and 9), and generally the observed range of the length of the guard in both species is between 50 mm and 100 mm.

The utility of means of "size"-parameters (Kermack, 1954, pp. 391–392), e.g. length, width, and breath of an animal, in palaeontological material may be the subject of discussion, because samples very often consist of growth-series with an unknown proportion of juvenile specimens. However, it should be understood that in belemnites, and many other fossil groups, criteria are not available for detecting the ontogenetic age of an individual, and especially it is not possible to discern at which size a belemnite specimen becomes adult.

The size-frequency distribution of the length of the guard of the sample of *A. plenus* indicates the number of preserved dead individuals in each size-class, and the mean of the length of the guard shows which size most of the specimens in the sample had reached when they died. In the present distribution, the mean and the mode (situated in the 75–80 mm size-class) are similar because the histogram is normally distributed. In cases with skewed distributions the mode is the more meaningful parameter.

Initially, the shape of the size-frequency distribution of fossil organisms is a function of the interplay of the growth-rate and the mortality-rate of the species (Craig & Hallam, 1963; Craig & Oertel, 1966; Craig, 1967). If it is possible to reduce or remove the taphonomic overprint and if the size-frequency distribution is uniform in all analysed samples, the shape and thus the mode can be considered of species diagnostic value.

The shape of the histogram and the mode of the sample of *A. plenus* may be meaningful for the species, and this can only be tested by analysing more samples of *A. plenus* from different localities. In this connexion it can be mentioned that Naidin (1964) reported that the mean of the length of the guard of *A. plenus* from the Russian Platform was c. 75 mm, which is consistent with the figure obtained on *A. plenus* from the Betchworth Limeworks.

It is obvious that the modes or means and the shape of the histograms should be considered carefully, because samples may be biased, e.g. by selective collection of large or small specimens, by post-mortem sorting, etc. Incidentally, means of "size"-parameters of samples of belemnites have been used succesfully analysing time-trends in evolutionary lineages, e.g. in the genus *Gonioteuthis* (Ernst, 1964) and in the species complex of *A. verus* (Reyment & Naidin, 1962).

Bivariate analyses (N = 114)

Regression analyses were made in order to study the growth relationship between pairs of variates. The regression lines were fitted by the least

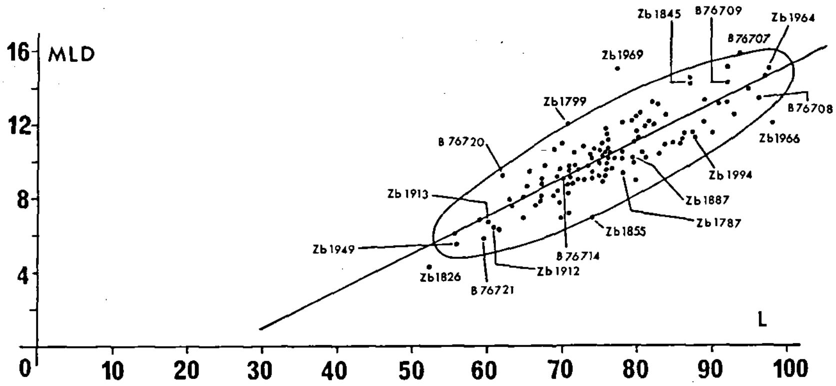


Fig. 3. Scatter diagram of the length of the guard (L) in mm versus the maximal lateral diameter (MLD) in mm and the regression line, fitted by the least squares method, for *A. plenus* from the Betchworth Limeworks.

squares method for reasons given in Christensen (1973). The regression line is written: y = a + bx, and the original measurements are used in the calculations because of the linear trend of the scatter plots on ordinary graph paper. The discussions below contain estimates of the following statistics: the slope (b) and the standard deviation (SD_b) of the slope; the intercept on the y-axis (a) and the standard deviation (SD_a) of the intercept; the standard deviation (SD_{yx}) of the regression line; and the correlation coefficient (r). The disadvantages of the use of ratios have been discussed by many authors, a review of which is given in Christensen (1973). Consequently the ratios commonly calculated in the belemnite literature, are not used in this paper. See also discussion below.

The correlation matrix is shown below.

$$\mathbf{R} = \begin{bmatrix} 1.000 & 0.879 & 0.874 & 0.862 \\ & 1.000 & 0.989 & 0.960 \\ & & 1.000 & 0.953 \\ & & & 1.000 \end{bmatrix}$$

The correlation coefficients are highly significant ($P < 0.001$) in all combinations of characters.

The following three regression analyses were made: 1) length of the guard (x) versus the maximal lateral diameter (y), 2) the maximal lateral diameter (x) versus the lateral diameter at the alveolar fracture (y), and 3) the dorso-ventral diameter at the alveolar fracture (x) versus the lateral diameter at the same place (y). The scatter plots of the three analyses are shown in figs 3–5, and the estimates of the statistical parameters for each analysis are given in table 1.

y = a + bx	SD_a	SD_b	SD_{yx}	t_a-test for 112 degrees of freedom	
				t_a-value	Probability
MLD = −5.1152 + 0.2020 L	0.8634	0.0112	1.1504	5.9243	P < 0.001
LDAF = 0.8669 + 0.6423 MLD	0.2031	0.0143	0.4633	4.2681	P < 0.001
LDAF = 0.3197 + 0.9018 DVDAF	0.1036	0.0128	0.2270	3.0843	0.005 > P > 0.001

Table 1. Estimates of the statistical parameters of the three regression analyses for the sample of *A. plenus* from the Betchworth Limeworks, and t-tests for the y-intercepts.

A t-test on the intercept on the y-axis for each analysis was made to see if the intercept differed significantly from zero (see table 1). In the three analyses, highly significant t-values were found. This means that the intercept is significantly different from zero, and therefore the relationships between the pairs of variates are allometric. A brief discussion of growth relationship (isometry versus allometry) is given in Christensen (1973).

The 95 % confidence ellipses for the observations were calculated in the way indicated in Sokal & Rohlf (1969, pp. 526–532), and are plotted on figs 3–5. As discussed above, specimens with a length of the guard less than c. 50 mm have existed, but since these guards are very seldom found in samples of *A. plenus*, it seems permissible to calculate the ellipses.

On the basis of the three scatter diagrams, the sample of *A. plenus* can be characterised as homogeneous.

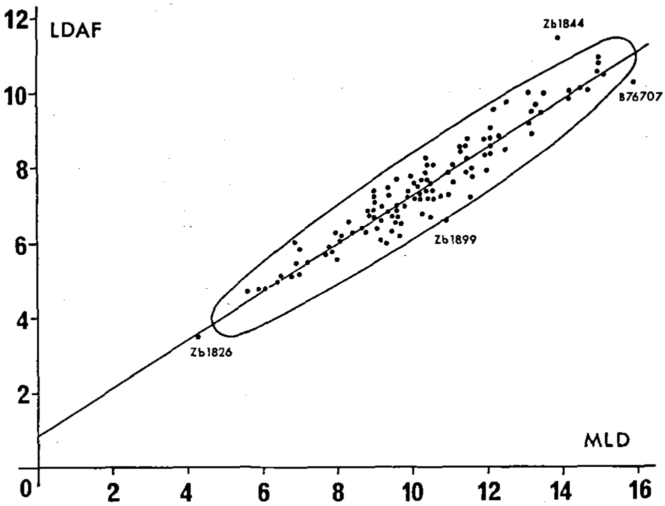


Fig. 4. Scatter diagram of the maximal lateral diameter (MLD) in mm versus the lateral diameter at the alveolar fracture (LDAF) in mm and the regression line, fitted by the least squares method, for *A. plenus* from the Betchworth Limeworks.

If we imagine that all the specimens shown in text-fig. 3 are projected onto the regression line, we can calculate the y-values for selected x-values and see how the ratios of the two characters will change during the growth of the belemnite.

x (L) (mm)	y (MLD) (mm)	$\frac{x}{y}$
50	4.984	10.00
60	7.004	8.57
70	9.023	7.76
80	11.043	7.24
90	13.063	6.89
100	15.083	6.63

The table clearly shows that the ratio between the length of the guard and the maximal lateral diameter changes during the growth and is of questionable value characterising a species. For example, a juvenile specimen in this sample could be classified easily as *A. primus,* whereas an adult specimen would be considered as *A. plenus* (see p. 13).

The three specimens (Zb 1969, Zb 1966, and Zb 1826) which fall outside the ellipse in fig. 3, and the three specimens (Zb 1855, Zb 1799, and B 76707) which lie in the periphery of it are figured on pl. 1, fig. 3, pl. 2, figs. 1 and 5, pl. 3, fig. 4, and pl. 4, figs. 1 and 3. An additional 13 specimens are figured to show the variation from slender specimens situated in the lower part of the ellipse to stout specimens situated in the upper part of the ellipse. The figured specimens and fig 3 illustrate that there is a gradual transition from slender to stout specimens.

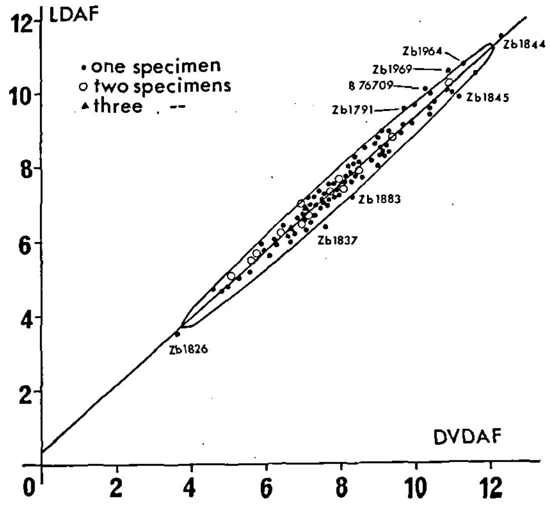


Fig. 5. Scatter diagram of the dorso-ventral diameter at the alveolar fracture (DVDAF) in mm versus the lateral diameter at the same place (LDAF) in mm and the regression line, fitted by the least squares method, for *A. plenus* from the Betchworth Limeworks.

In the regression analyses of the maximal lateral diameter versus the lateral diameter at the alveolar fracture and the dorso-ventral diameter at the alveolar fracture versus the lateral diameter at the same place, the ratios of the pairs of variates will become steadily larger during the growth of the belemnite, so that the use of these ratios for characterising a species also can be considered of little taxonomic value.

The ellipse in fig. 5 is very compressed because of the very high correlation coefficient ($r = 0.989$). It was found that the dorso-ventral diameter was equal to or larger than the lateral diameter in all specimens, except in B 76721, where the dorso-ventral diameter is 4.6 and the lateral diameter is 4.7 mm.

Quadrivariate principal component analyses (N = 114)

A principal component analyses (PCA) of the dispersion (variance-covariance) matrix was obtained with an ALGOL program prepared by Dr. A. S. Horowitz for the Aarhus University CDC 6400 computer. The purpose of the PCA was to examine the residual variability in the sample as represented by the component scores in order to determine if any clustering could be observed in an otherwise homogeneous sample. The dispersion matrix is as follows.

$$
\mathbf{S} = \begin{bmatrix} 92.561 & 14.105 & 12.783 & 18.696 \\ & 2.780 & 2.507 & 3.610 \\ & & 2.312 & 3.268 \\ & & & 5.088 \end{bmatrix}
$$

The dispersion matrix yielded the eigenvalues (latent or characteristic roots) and the eigenvectors shown in table 2.

The first principal component accounts for almost all of the variation (97.75 %), and is interpreted as representing size variation of the guard (L). This interpretation is consistent with similar interpretations generally given in biologic studies (Blackith & Reyment, 1971, pp. 147–150). The

Eigenvalues	percentages of total variation	VARIATES				Eigenvectors
		L	DVDAF	LDAF	MLD	
100.4289	97.75	0.9592	0.1494	0.1353	0.1984	I
2.0813	2.03	-0.2825	0.4777	0.4372	0.7077	II
0.2030	0.20	-0.0141	0.4992	0.5409	-0.6768	III
0.0266	0.02	0.0018	-0.7073	0.7057	0.0422	IV

Table 2. The eigen-values and the eigen-vectors of the PCA for the sample of *A. plenus* from the Betchworth Limeworks.

contribution of the remaining characters to the first principal component is roughly of the same magnitude.

The second principal component accounts for 2 % of the total variance and can be related to shape variation of the guard (MLD, DVDAF, and LDAF). The contribution of DVDAF and LDAF to the second principal component are approximately of the same order, and L is negatively correlated with the remaining characters.

The third and fourth component likewise can be related to shape variation of the guard (MLD, LDAF, and DVDAF).

The plots of the principal components scores of the transformed variates on the first and second, first and third, first and fourth, second and third, second and fourth, and third and fourth principal axis did not reveal any clustering, and the sample is regarded as homogeneous, which is consistent with the bivariate analyses.

The outprint of the PCA-program (including the plots of the transformed variables) can be obtained from the author on request.

Systematic position of *A. primus* and *A. plenus*

The second part of the paper evaluates the mutual relationship between *A. primus* and its subspecies, *A. plenus* and its subspecies, and *A. primus* and *A. plenus*. As mentioned above (p. 2) *A. primus* is said to differ from *A. plenus* in being smaller and more slender, and it is not swollen posteriorly. To facilitate the understanding of the following discussion synonyms for *A. primus* and *A. plenus* respectively are given below.

Actinocamax primus Arkhangelsky, 1912.

1829 *Belemnites lanceolatus* Sowerby, p. 208, pl. 600, figs. 8–9 (non Schlotheim, 1813).
1896 *Belemnitella lanceolata* (Sowerby); Jukes-Browne & Hill, p. 163.
1903 *Actinocamax lanceolatus* (Sowerby); Jukes-Browne & Hill, p. 26.
1904 *Actinocamax lanceolatus* (Sowerby); Jukes-Browne & Hill, p. 470.
1912 *Actinocamax primus* Arkhangelsky, p. 578, pl. 10, figs. 1–5.
1912 *Actinocamax primus* var. *elongatus* Arkhangelsky, p. 581.
1948 *Actinocamax primus* Arkhangelsky; Jeletzky, p. 340, text-fig. 1.
1948 *Actinocamax primus* var. *elongatus* Arkhangelsky; Jeletzky, p. 340, text-fig. 2.
1957 *Actinocamax primus primus* Arkhangelsky; Birkelund, p. 9, pl. 1, figs. 1,2,4.
1957 *Actinocamax primus elongatus* Arkhangelsky; Birkelund, p. 12, pl. 1, fig. 3.
1958 *Actinocamax primus* Arkhangelsky; Hancock, p. 175.
1961 *Actinocamax primus* var. *elongatus* Arkhangelsky; Hancock, p. 14.
1964 *Actinocamax primus primus* Arkhangelsky; Naidin, p. 56, pl. 1, fig. 9; pl. 2, figs. 3,4,7.

1964 *Actinocamax primus curtus* Naidin, p. 61, pl. 2, figs. 5,6.
?1970 *Actinocamax* cf. *primus* Arkhangelsky; Kennedy, p. 656.
?1970a *Actinocamax primus* Arkhangelsky; Christensen, p. 70, text-figs. 2A-C.
?1970b *Actinocamax* cf. *primus* Arkhangelsky; Christensen, p. 503, text-fig. 2.

Actinocamax plenus (Blainville, 1825).

1825 *Belemnites plenus* Blainville, p. 376.
1827a *Belemnites plenus* Blainville; Blainville, pl. 11 bis, fig. 3.
1827b *Belemnites plenus* Blainville; Blainville, p. 59, pl. 1, fig. 6.
1853 *Belemnitella plena* (Blainville); Sharpe, p. 9, pl. 1, figs. 12–16.
1876 *Actinocamax plenus* (Blainville); Schlüter, p. 186, pl. 52, figs. 16–19.
1896 *Belemnitella plena* (Blainville); Jukes-Browne & Hill, p. 163.
1903 *Actinocamax plenus* (Blainville); Jukes-Browne & Hill, p. 26, text-fig. 10.
1948 *Actinocamax plenus* (Blainville); Jeletzky, p. 342, text-figs. 3,4.
1952 *Actinocamax plenus* (Blainville); Naidin, p. 60, text-fig. 20.
1958 *Actinocamax plenus* var. *sinzowi* Nikitin, p. 7, pl. 2, fig. 16.
1964 *Actinocamax plenus plenus* (Blainville); Naidin, p. 43, pl. 1, figs. 1,2; pl. 2, figs. 1,2.
1964 *Actinocamax plenus triangulus* Naidin, p. 48, pl. 1, figs. 5–7; text-fig. 9.
1964 *Actinocamax plenus longus* Naidin, p. 49, pl. 1, fig. 4; text-figs. 9,10.
1964 *Actinccamax plenus acutus* Naidin, p. 50, pl. 1, fig. 3; text-fig. 7.
?1964 *Actinocamax plenus contractus* Naidin, p. 46, pl. 3, fig. 3.
?1954 *Actinocamax plenus crassus* Naidin, p. 46, pl. 3, figs. 1,2; text-fig. 9.

Nikitin (1958) erected *A. plenus sinzowi* and reported the subspecies from England, the Wolga area, and the Dniepr-Donez syneclise. According to Nikitin this subspecies differs from *A. p. plenus* in having a shallow pseudoalveolus, but as seen in the sample of *A. p. plenus* from the Betchworth Limeworks about 7 % of the specimens have a shallow pseudoalveolus, and there is a gradual transition from specimens with a pseudoalveolus to specimens with an alveolar fracture. Consequently, the presence of a pseudoalveolus is not regarded as a diagnostic character, and the subspecies *sinzowi* is placed in synonymy.

Arkhangelsky (1912) established *A. primus elongatus* and stated that it differs from *A.p. primus* in its very elongated subcylindrical guard. Arkhangelsky, however, reported that there is a gradual transition from typical *A.p. primus* to typical *A.p. elongatus*. Jeletzky (1948, text-figs. 1 and 2) figured *A.p. primus* and *A.p. elongatus,* which came from the same zone at the same locality, and Birkelund (1957) described *A.p. primus* and *A.p. elongatus* from the Arnager Greensand. Birkelund (op. cit. p. 13), however, stated that: "Their common stratigraphical occurrence and their morphological features makes the distinction between these two subspecies doubtful". Because the International Code of Zoological Nomenclature only accepts chronological and geographical subspecies, the recognition of the subspecies *elongatus* does not seem justified.

Naidin (1964) created five new subspecies of *A. plenus,* viz. *contractus,*

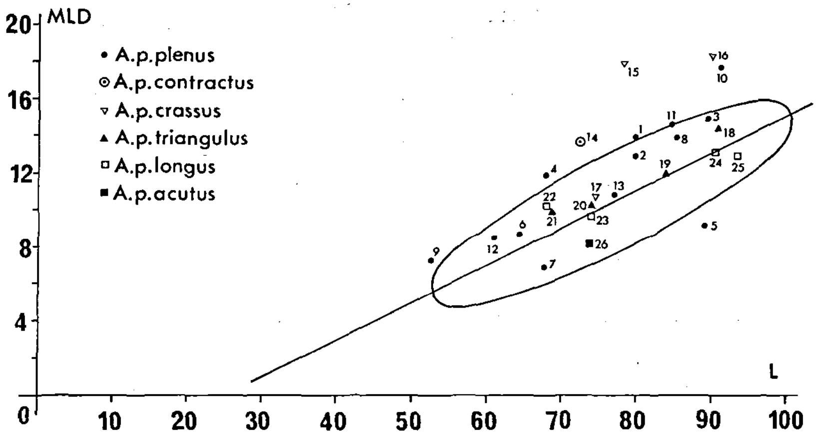


Fig. 6. Scatter diagram of the length of the guard (L) in mm versus the maximal lateral diameter (MLD) in mm for *A. plenus plenus* (nos. 1–13), *A. plenus contractus* (no. 14), *A. plenus crassus* (nos. 15–17), *A. plenus triangulus* (nos. 18–21), *A. plenus longus* (nos. 22–25), and *A. plenus acutus* (no. 26). The regression line and the 95% confidence ellipse for the observations of the sample of *A. plenus* from the Betchworth Limeworks are also shown.

1: Holotype, Blainville (1827a, pl. 11 bis, fig. 3). 2: Blainville (1827b, pl. 1, fig. 6). 3: Sharpe (1853, pl. 1, fig. 15). 4: Sharpe (1853, pl. 1, fig. 12). 5: Schlüter (1876, pl. 52, fig. 19). 6: Schlüter (1876, pl. 52, fig. 16). 7: Schlüter (1876, pl. 52, fig. 17). 8: Jeletzky (1948, text-fig. 3). 9: Jeletzky (1948, text-fig. 4). 10: Naidin (1964, pl. 2, fig. 1). 11: Naidin (1964, no. 170/10). 12: Naidin (1964, no. 170/3). 13: Naidin (1964, pl. 2, fig. 2). 14: Naidin (1964, pl. 3, fig. 3). 15: Naidin (1964, pl. 3, fig. 1). 16: Naidin 1964, pl. 3, fig. 2). 17: Naidin (1964, no. 5305/13). 18: Naidin (1964, pl. 1, fig. 6). 19: Naidin (1964, pl. 1, fig. 7). 20: Naidin (1964, no. 1745/2). 21: Naidin (1964, no. 8023/3). 22: Naidin (1964, no. 5/3). 23: Naidin (1964, no. 901/4). 24: Naidin (1964, pl. 1, fig. 4). 25: Naidin (1964, no. 6/5). 26: Naidin (1964, pl. 1, fig. 3).

crassus, triangulus, longus, and *acutus,* and one new subspecies of *A. primus,* viz. *curtus.* The subspecies were briefly described without accompanying diagnostic differentiations and were characterised by various ratios, such as the length of the guard divided by the maximal lateral diameter, the maximal lateral diameter divided by the lateral diameter at the alveolar fracture, etc. For example, according to Naidin, *A. primus* is characterised by having a ratio of the length of the guard divided by the maximal lateral diameter, which is between 7.0 and 12.5, while the same ratio in *A. plenus* is between 4.5 and 7.0. As shown in the first part of the paper the use of ratios is of little taxonomic value owing to the allometric relationships between the pairs of variates. A consequence of the differentiation between *A. primus* and *A. plenus* given by Naidin is that about the half of the sample of *A. plenus* from the Betchworth Limeworks should be classified as *A. primus* (cf. p. 9).

Because Naidin gave measurements of the figured specimens of *A. primus* and *A. plenus,* and some additional specimens, the length of the guard versus the maximal lateral diameter, the maximal lateral diameter versus the lateral diameter at the alveolar fracture, and the dorso-ventral diameter at the alveolar fracture versus the lateral diameter at the same place, were plotted in figs 6–8 for *A. plenus* and in figs 9–11 for *A. primus.* Some other specimens of *A. primus* and *A. plenus* are also indicated in these text-figures (cf. explanations to figs 6 and 9). The measurements based on figured specimens naturally are encumbered with a certain unreliability. The regression lines and the 95 % confidence ellipses for the observations of the sample of *A. plenus* from the Betchworth Limeworks are also indicated in figs 6–11.

Two specimens of *A. plenus crassus* (nos. 15 and 16) fall outside the three ellipses shown in figs 6–8, and one specimen (no. 17) lies in the central part of the three ellipses. Naidin described 23 complete specimens and some fragments of *A.p. crassus* from the Wolgograd area, but he only gave measurements of these three specimens. On the basis of the three specimens it is not clear if they represent a subspecies or only are extreme variants of *A. plenus.*

A. plenus contractus (no. 14) falls outside the ellipses shown in figs 6 and 8. *A.p. contractus* was established on one complete specimen and

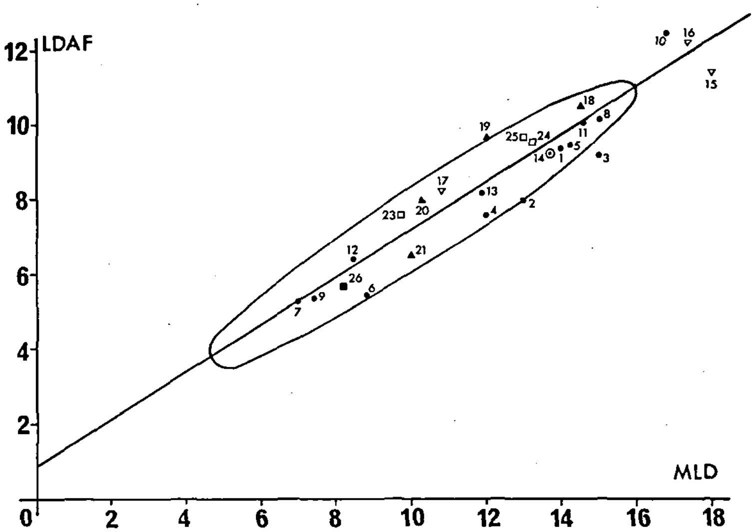


Fig. 7. Scatter diagram of the maximal lateral diameter (MLD) in mm versus the lateral diameter at the alveolar fracture (LDAF) in mm of *A. plenus.* Same symbols for the specimens as in fig. 6. The regression line and the 95% confidence ellipse for the observations for the sample of *A. plenus* from the Betchworth Limeworks are also plotted.

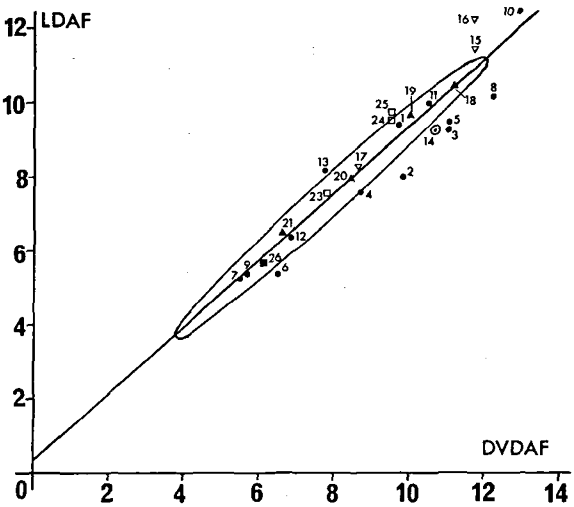


Fig. 8. Scatter diagram of the dorso-ventral diameter at the alveolar fracture (DVDAF) in mm versus the lateral diameter at the same place (LDAF) in mm for *A. plenus*. Same symbols for the specimens as in fig. 6. The regression line and the 95% confidence ellipse for the observations for the sample of *A. plenus* from the Betchworth Limeworks are also drawn.

some fragments from the Chernogow area on the Russian Platform. This specimen may represent a subspecies of *A. plenus,* but it seems equally reasonable to assume that the specimen is a morphological variant of *A. plenus.*

The remaining three subspecies of *A. plenus* proposed by Naidin, *triangulus, longus,* and *acutus,* all lie within the variation of *A. plenus* from the Betchworth Limeworks. Furthermore, the short descriptions given by Naidin do not contain characters, which can be regarded as diagnostic. Consequently, the three subspecies are not recognised and are placed in synonymy.

Some specimens of *A.p. plenus* from Europe and Transcaspian lie outside the ellipse of *A.p. plenus* from the Betchworth Limeworks. For example, specimen no. 10 (Naidin, 1964, pl. 2, fig. 1) falls outside of all the three ellipses. It lies, indeed, very close to *A.p. crassus* (no. 16) in the three text-figures, but I prefer to consider the specimen a morphological variant of *A.p. plenus* rather than refer it to *A.p. crassus.*

The scatter diagram of *A.p. primus, A.p. elongatus,* and *A.p. curtus* are shown in figs 9–11. Some of the specimens shown in fig. 9 are not plotted in figs 10–11, because all four measurements could not be obtained on all specimens. It is quite evident that most of the specimens of *A. primus* lie within the three ellipses. Two juvenile specimens of *A.p. primus* (nos. 3 and 5) fall outside the ellipse in fig. 9, and this results

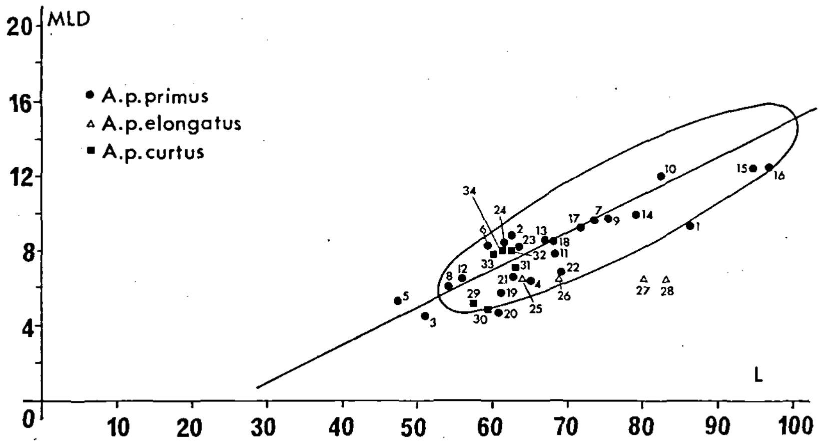


Fig. 9. Scatter diagram for the length of the guard (L) in mm versus the maximal lateral diameter (MLD) in mm for *A. primus primus* (nos. 1–24), *A. primus elongatus* (nos. 25–28), and *A. primus curtus* (nos. 29–34). The regression line and the 95% confidence ellipse for the observations of the sample of *A. plenus* from the Betchworth Limeworks are also indicated.

1: Sowerby (1829, pl. 600, fig. 8). 2: Jeletzky (1948, text-fig. 1). 3: Arkhangelsky (1912, no. 1). 4: Arkhangelsky (1912, no. 2). 5: Arkhangelsky (1912, no. 4). 6: Arkhangelsky (1912, no. 5). 7: Arkhangelsky (1912, no. 6). 8: Naidin (1964, no. 296). 9: Naidin (1964, no. 5286/5). 10: Naidin (1964, no. 5286/3). 11: Naidin (1964, no. 151/1). 12: Naidin (1964, no. 7259/1). 13: Naidin (1964, no. 7240/6). 14: Naidin (1964, pl. 2, fig. 4). 15: Naidin (1964, pl. 2, fig. 3). 16: Birkelund (1957, pl. 1, fig. 1). 17: Birkelund (1957, no. 2). 18: Birkelund (1957, no. 4). 19: Birkelund (1957, no. 8). 20: Birkelund (1957, no. 9). 21: Birkelund (1957, no. 6). 22: Birkelund (1957, pl. 1, fig. 2). 23: Birkelund (1957, no. 5). 24: Birkelund (1957, pl. 1, fig. 4). 25: Jeletzky (1948, text-fig. 2). 26: Arkhangelsky (1912, no. 3). 27: Specimen from Cave-Hill, Ireland, Naidin (1964). 28: Specimen from Cave-Hill, Ireland, Naidin (1964). 29: Naidin (1964, pl. 2, fig. 6). 30: Naidin (1964, no. 12/28). 31: Naidin (1964, no. 12/18). 32: Naidin (1964, no. 12/8). 33: Naidin (1964, no. 12/12). 34: Naidin (1964, pl. 2, fig. 5).

from the small size of the guard as the specimens lie very near the regression line. Two specimens referred to as *A.p. elongatus* (nos. 27 and 28) from northern Ireland fall outside the ellipse in fig. 9, whereas two other specimens (nos. 25 and 26) lie inside the ellipse. As noted earlier it seems reasonable to regard the very slender specimens of *A. primus* as variants, because there is a gradual transition from *A.p. primus* to *A.p. elongatus.* In this connexion it should be mentioned that only very few specimens ascribed to *A.p. elongatus* are reported in the literature. Arkhangelsky (1912), Jeletzky (1948), and Birkelund (1957) each recorded one specimen. According to Naidin (1964) the subspecies has not been encountered in the Russian collections studied by him. On the other hand,

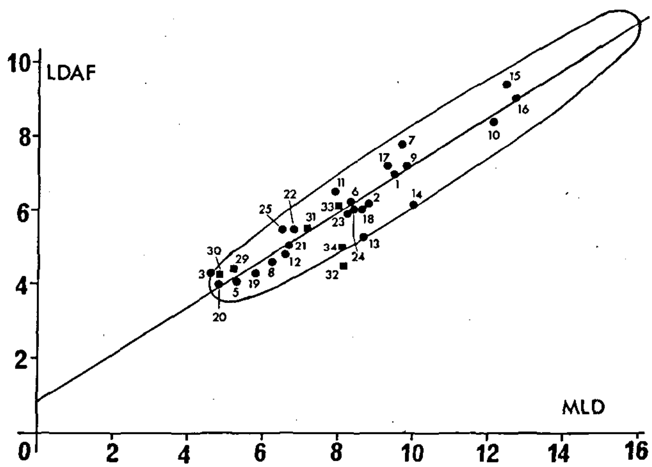


Fig. 10. Scatter diagram of the maximal lateral diameter (MLD) in mm versus the lateral diameter at the alveolar fracture (LDAF) in mm for *A. primus*. Same symbols for the specimens as in fig. 9. The regression line and the 95% confidence ellipse for the observations of the sample of *A. plenus* from the Betchworth Limeworks are also plotted.

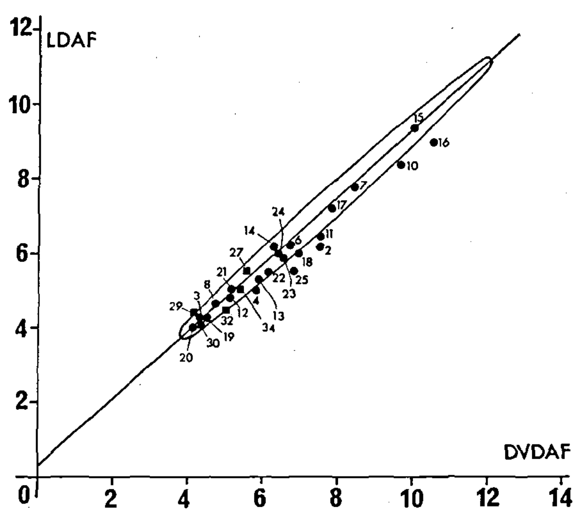


Fig. 11. Scatter diagram of the dorso-ventral diameter at the alveolar fracture (DVDAF) in mm versus the lateral diameter at the same place (LDAF) in mm for *A. primus*. Same symbols for the specimens as in fig. 9. The regression line and the 95% confidence ellipse for the observations of the sample of *A. plenus* from the Betchworth Limeworks are also drawn.

Naidin obtained two plaster casts of the subspecies from northern Ireland (plotted as nos. 27 and 28 in fig. 9 in the present paper). These specimens are also mentioned in Hancock (1961, p. 14), and according to Hancock (loc. cit.) they should be very similar to the slender fragment of *A.p. elongatus* figured in Birkelund (1957, pl. 1, fig. 3).

The plots of *A.p. curtus* clearly show that there are no differences between this subspecies and *A.p. primus* and the subspecies *curtus* is synonymised.

It is remarkable that most of the specimens of *A. primus* are situated in the lower half of the ellipses in figs 9–11. Since the length of the guard is correlated with the maximal lateral diameter, the dorso-ventral diameter at the alveolar fracture, and the lateral diameter at the same place, only the difference in the length of the guard between *A. primus* and *A. plenus* will be discussed.

A histogram of the length of the guard based on the 34 specimens plotted in fig. 9 is shown in fig. 12. The size-frequency distribution is right-skewed with a mode in the 60–65 mm size-class and the observed range is 45 mm to 100 mm. The histogram should be considered with great reservation because it is based on specimens from different places in Europe. It is, unfortunately, not possible to test this histogram, since measurements of large samples of *A. primus* have not been published. However, according to previous descriptions of *A. primus* stating that the observed range of the length of the guard of *A. primus* and *A. plenus* is similar and the length of the guard of *A. primus* is smaller than in *A. plenus,* a right-skewed distribution seems most likely. The mode in the 60–65 mm size-class indicates that most specimens had grown to that size when they died.

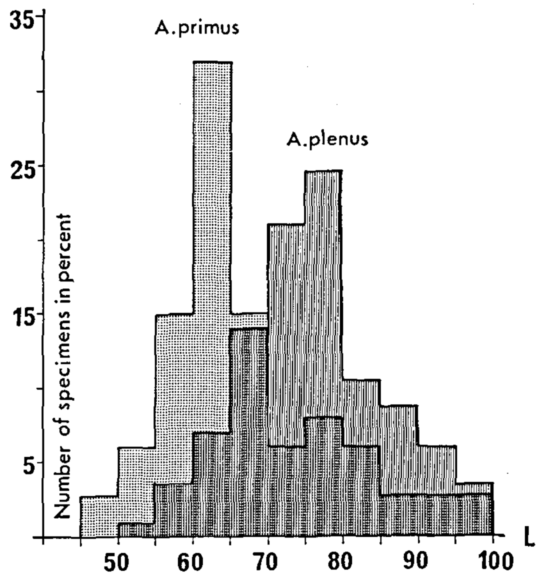
Provided that the size-frequency distributions of *A. primus* and *A. plenus* shown in fig. 12 are typical for the two species, the shape of the two histograms reflects that the interaction of the growth-rate and the mortality-rate is different in the two species.

On the basis of the difference of the modes of the length of the guard in *A. plenus* and *A. primus* and the presumed dissimilarity of the size-frequency distributions of the two species, compared with that *A. primus* appears earlier in the geological record than *A. plenus* (see p. 22), it seem justified to retain the species *primus*.

Stratigraphy

According to Jeletzky (1948) *A. primus* occurs in the Lower Cenomanian (*Schloenbachia varians* Zone) and in the lowermost part of the Upper Cenomanian (*Holaster subglobosus* Zone), and is followed upwards by *A.*

Fig. 12. Histogram of the length of the guard in mm (L) of *A. primus*. The histogram is based on the 34 specimens of *A. primus* plotted in fig. 9. The histogram of *A. plenus* from the Betchworth Limeworks is superimposed, and the area with both signatures indicates the degree of overlapping of the two histograms.



plenus from the Upper Cenomanian and the Lower Turonian (*Inoceramus labiatus* Zone). Jeletzky's survey was based on the available knowledge of the stratigraphical distribution of the two species in England, France, Germany, Russia, and Czechoslovakia.

As mentioned earlier (p. 3), Jefferies (1961) showed that *A. plenus* in the Anglo-Paris Basin is restricted to beds 4–6 of the *A. plenus* Marls. The age of the *A. plenus* Zone has been the subject of much discussion, which is reviewed by Schmid (1965) and more recently by Kennedy & Juignet (1973). The different opinions of the age of the *A. plenus* Zone are partly due to the fact that there was supposed to be a stratigraphical gap, corresponding to the *A. plenus* Zone, between the type Cenomanian and the type Turonian (C. W. Wright, J. M. Hancock et al. in Basse, 1959). Therefore, Tröger (1961, 1968, 1969) and Christensen (1973) referred the *A. plenus* Zone in Bohemia, Saxony, and Scania, respectively, to the passage beds between the Upper Cenomanian and the Lower Turonian. Jefferies (1963) regarded the *A. plenus* Horizon as a subzone of the *I. labiatus* Zone, but Hancock (in Jefferies, 1963, p. 31) recommended that the *A. plenus* Horizon be regarded as a zone in its own right. Hancock (1969) and Kennedy & Hancock (1970) placed the *A. plenus* Zone in the upper Upper Cenomanian but without discussion. However, recent studies by Kennedy & Juignet (1973) in the type area of the Cenomanian in France have shown that the *Metoicoceras gourdoni* Zone (= Jefferies' beds 4–8 of the *A. plenus* Marls) is present within the type Cenomanian.

WESTERN EUROPE				U.S.S.R.		
STAGES		ZONES		ZONES	STAGES	
LOWER TURONIAN		INOCERAMUS LABIATUS/ MAMMITES NODOSOIDES		INOCERAMUS LABIATUS	UPPER	LOWER TURONIAN
				ACTINOCAMAX P. TRIANGULUS with I. labiatus and M. nodosoides	LOWER	
CENOMANIAN	UPPER	HORIZON A with I. ex gr. pictus	?	SCAPHITES EQUALIS with I. pictus	UPPER	CENOMANIAN
		ACTINOCAMAX PLENUS				
		CALYCOCERAS NAVICULARE				
	MIDDLE	ACANTHOCERAS RHOTOMAGENSE				
	LOWER	MANTELLICERAS MANTELLI	?	EXOGYRA CONICA	LOWER	

Table 3. Stratigraphical correlation diagram of the Cenomanian and the Lower Turonian. The diagram is based on Hancock (1959, 1969), Kennedy (1969, 1970), Kennedy & Hancock (1970), and Kennedy & Juignet (1973) for the western Europe succession and Naidin (1964) for the U.S.S.R. succession. Horizon A of Kennedy & Juignet (1973) is characterised by *I.* ex gr. *pictus* and corresponds to the stratigraphical sequence in England and France between th top of the *A. plenus* Zone and the lowest appearance of *I. labiatus*. Naidin (1964) listed *I. pictus* from the *S. equalis* Zone and *I. labiatus* and *M. nodosoides* from the *A.p. triangulus* Zone.

Furthermore, they showed that *I. labiatus* is absent from the *A. plenus* Marls and the most convenient level for the base of the Turonian is the base of the *Mammites nodosoides/Inoceramus labiatus* Zone (see table 3).

It is worth noting that Tröger (1968, p. 6) reported that *A. plenus* never has been found together with *I. labiatus* in Bohemia and Saxony, and the single specimen of *A. plenus* from the "Rotpläner" in Lower Saxony discussed by Schmid (1965) likewise was found in beds below the first occurrence of *I. labiatus.*

Naidin (1964, table 36) established the zone of *A. plenus triangulus* (= *A.p. plenus*) in the lower Lower Turonian below the *I. labiatus* Zone, but he listed *I. labiatus* and *M. nodosoides* from the *A.p. triangulus* Zone (see table 3). According to Naidin (op. cit.) *A.p. plenus, A.p. longus,* and *A.p. acutus* appear in the late Upper Cenomanian (upper part of the *S. equalis* Zone) and continue into the *A.p. triangulus* Zone, whereas *A.p. contractus, A.p. triangulus,* and *A.p. crassus* are confined to the *A.p. triangulus* Zone. It should be noted that *A.p. longus, A.p. acutus, A.p. triangulus* are considered synonyms of *A.p. plenus* and *A.p. crassus* and *A.p. contractus* may very well be extreme morphological variants of *A. plenus.*

Therefore, *A. plenus* seems to appear at the same time in western and central Europe and the Russian Platform, but apparently it continues into the Lower Turonian on the Russian Platform. The discrepancy of the stratigraphical distributions may be real, but it may be due equally well to inadequate stratigraphical knowledge of the Russian specimens or different concept of the *Inoceramus* and ammonite species used as index fossils.

Very little is known about the stratigraphic range of *A. primus* in western Europe because 1) the species has not been reviewed recently, and 2) its rareness. Furthermore, the former division of the Cenomanian into two zones, the *Schloenbachia varians* Zone below and the *Holaster subglobosus* Zone above, is no longer tenable. According to Kennedy (1969, pp. 461–462) *S. varians* as interpreted by Jukes-Browne & Hill (1903, 1904) was used for all species of the genus *Schloenbachia,* which ranges through most of the Cenomanian, and *H. subglobosus* likewise ranges through the Cenomanian and has even been found in the uppermost Albian.

The two specimens of *A. primus* figured by Sowerby (1829), one of which was collected by Dr. Mantell, were said to come from Hamsey in Sussex. According to Jukes-Browne & Hill (1903, p. 64) the chalk exposed to Mantell ranged over parts of the Lower and Middle Chalk (= Cenomanian and Turonian). Jukes-Browne and Hill (1896, p. 163) reported *Belemnitella lanceolata* Sowerby (= *A. primus*) from Bed A (Lower Cenomanian, cf. Kennedy, 1970, p. 657) of Devon. Jukes-Browne & Hill

(1903, p. 26), in their general stratigraphic summary, listed *A. lanceolatus* (Sowerby) (= *A. primus*) from the *S. varians* Zone and *A. plenus* from the *H. subglobosus* Zone. In the following year Jukes-Browne & Hill (1904, p. 470) recorded *A. lanceolatus* from both the *S. varians* Zone and the *H. subglobosus* Zone, and *A. plenus* was cited from the *H. subglobosus* Zone and the *A. plenus* Zone. Although the former division of the Cenomanian is not accepted, *A. primus* apparently appears earlier than *A. plenus*.

Hancock (1961) described *A. primus elongatus* from the Lower Cenomanian (*Mantelliceras mantelli* Zone) at Antrim in Ireland. Hancock (1958) recorded *A. primus* from the *A. plenus* Zone at Reigate (Surrey) and Kennedy (1970) listed *A.* cf. *primus* from deposits of probably *A. plenus* Zone age at the Membury outlier in Devon.

Naidin (1964) divided the Cenomanian into two zones, the *Exogyra conica* Zone below and the *Scaphites equalis* Zone above, and he described *A. primus* from the upper part of the *E. conica* Zone and the lower part of the *S. equalis* Zone. He also cited *Acanthoceras rhotomagense* from the *S. equalis* Zone. According to Hancock (1959) and Kennedy (1970) *A. rhotomagense* is an index fossil of the Middle Cenomanian of England and France, and Kennedy (op. cit.) reported that *S. equalis* is found commonly in the lower part of the *A. rhotomagense* Zone. Therefore, the lower part of the Upper Cenomanian of Naidin presumably corresponds to parts of the Middle Cenomanian in England and France.

On the basis of this review of the stratigraphic range of *A. primus* it may be concluded that *A. primus* appears in the Lower Cenomanian and continues into Middle Cenomanian. The specimens of *A. primus* in the *A. plenus* Zone probably are slender specimens of *A. plenus*.

General conclusions

A review of the literature indicates that *A. primus* appears in the Lower Cenomanian and continues into the Middle Cenomanian, whereas *A. plenus* in western and central Europe is confined to the *A. plenus* Zone of Late Cenomanian age. On the Russian Platform, *A. plenus* starts in the late Upper Cenomanian and continues into the Lower Turonian, but the discrepancy in the stratigraphical distributions may be due to inadequate stratigraphical knowledge of the Russian specimens or a different species concept of the *Inoceramus* and ammonites used as index fossils.

According to the present study, the differences between the two species are apparently the modes of the length of the guard and the size-frequency distributions. On the basis of these differences and chronological position the species *A. primus* is valid.

It should be stressed that it is not possible on the basis of only a few specimens of *Actinocamax* to assign the specimens safely either to *A. primus* or *A. plenus*. In the opinion of the author one should have a representative sample (10–20 specimens) to make a reliable determination.

Two subspecies of *A. primus,* viz. *elongatus* and *curtus,* and four subspecies of *A. plenus,* viz. *sinzowi, triangulus, longus,* and *acutus,* are placed in synonymy. Further studies on *A. plenus* from Russia are necessary to determine if *A.p. crassus* and *A.p. contractus* are morphological variants, or whether the specimens should be retained as new subspecies as proposed by Naidin (1964).

The present study deals with the variation of a large sample of *A. plenus* from a well-known stratigraphic level, and it is my hope that this study be followed by similar studies on samples of *Actinocamax* from the Cenomanian in order to test the hypothesis advanced by Jeletzky (1948, p. 343) that *A. primus* and *A. plenus* are linked by a continuous suite of intermediate forms.

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I wish especially to thank A. S. Horowitz, who prepared the PCA-program, for highly inspiring discussions about statistical problems connected with the present study.

Dansk sammendrag

En population bestående af 114 eksemplarer af *Actinocamax plenus* fra Plenus-merglen i England (Betchworth Limeworks, Surrey) er blevet undersøgt variations-statistisk ved monovariable, bivariable, og multivariable statistiske metoder.

På basis af denne undersøgelse vises, at tre underarter af *A. plenus* og én underart af *A. primus,* opstillet af Naidin (1964), ikke kan opretholdes. Det vises endvidere, at *A. primus elongatus* Arkhangelsky og *A. plenus sinzowi* Nikitin ligeledes ikke kan opretholdes, da de hverken er geografiske eller kronologiske underarter.

Den observerede variation af rostrumlængden af *A. primus* og *A. plenus* er fundet at være identisk, 50–100 mm. Modus af rostrumlængden af de to arter er dermod tilsyneladende forskellig, ca. 60–65 mm hos *A. primus* og 75–80 mm hos *A. plenus.*

A. primus forekommer i Nedre Cenomanien og fortsætter op i Mellem Cenomanien, medens *A. plenus* i Vest- og Central-Europa kun forekommer i *A. plenus* Zonen i Øvre Cenomanien. På den Russiske platform starter *A. plenus* i øvre del af Øvre Cenomanien og fortsætter tilsyneladende op i Nedre Turonien.

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Plate 1

All figures are of natural size unless otherwise indicated. Specimens are coated with ammonium chloride.

Figs. 1–3. *Actinocamax plenus* (Blainville, 1825) from the Plenus Marls of the Betchworth Limeworks. A: Dorsal view. – B: Lateral view. – C: Ventral view. – D: View of the adoral part of the guard. 1: Zb 1964. – 2: B 76708. – 3: Zb 1966. Figs 2D and 3D, × 2.

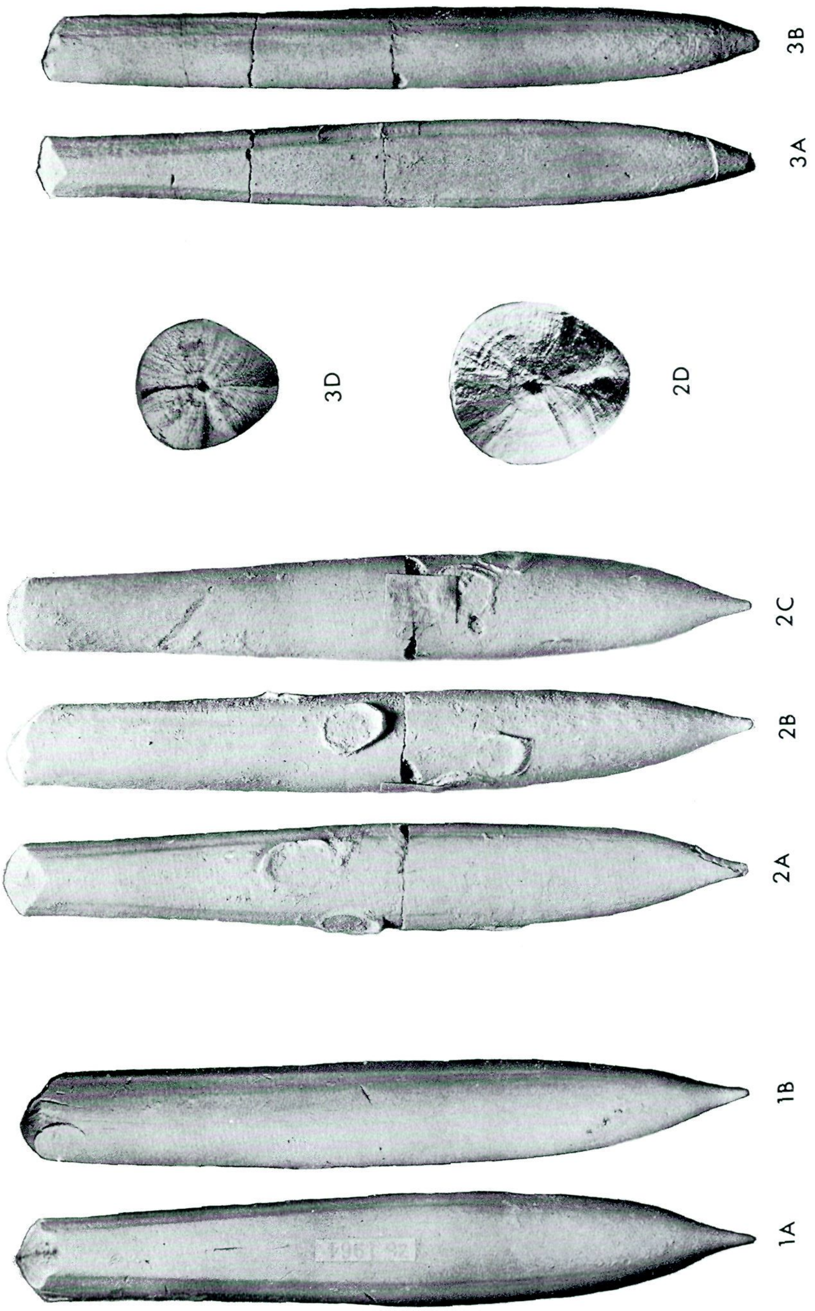

3B
3A
3D
2D
2C
2B
2A
1B
1A

Plate 2

All figures are of natural size unless otherwise indicated. Specimens are coated with ammonium chloride.

Figs. 1–5. *Actinocamax plenus* (Blainville, 1825) from the Plenus Marls of the Betchworth Limeworks. A: Dorsal view. – B: Lateral view. – C: Ventral view. – D: View of the adoral part of the guard. – 1: B 76707. – 2: Zb 1994. – 3: Zb 1845. – 4: Zb 1949. – 5. Zb 1826. Figs 2D and 3D, × 2.

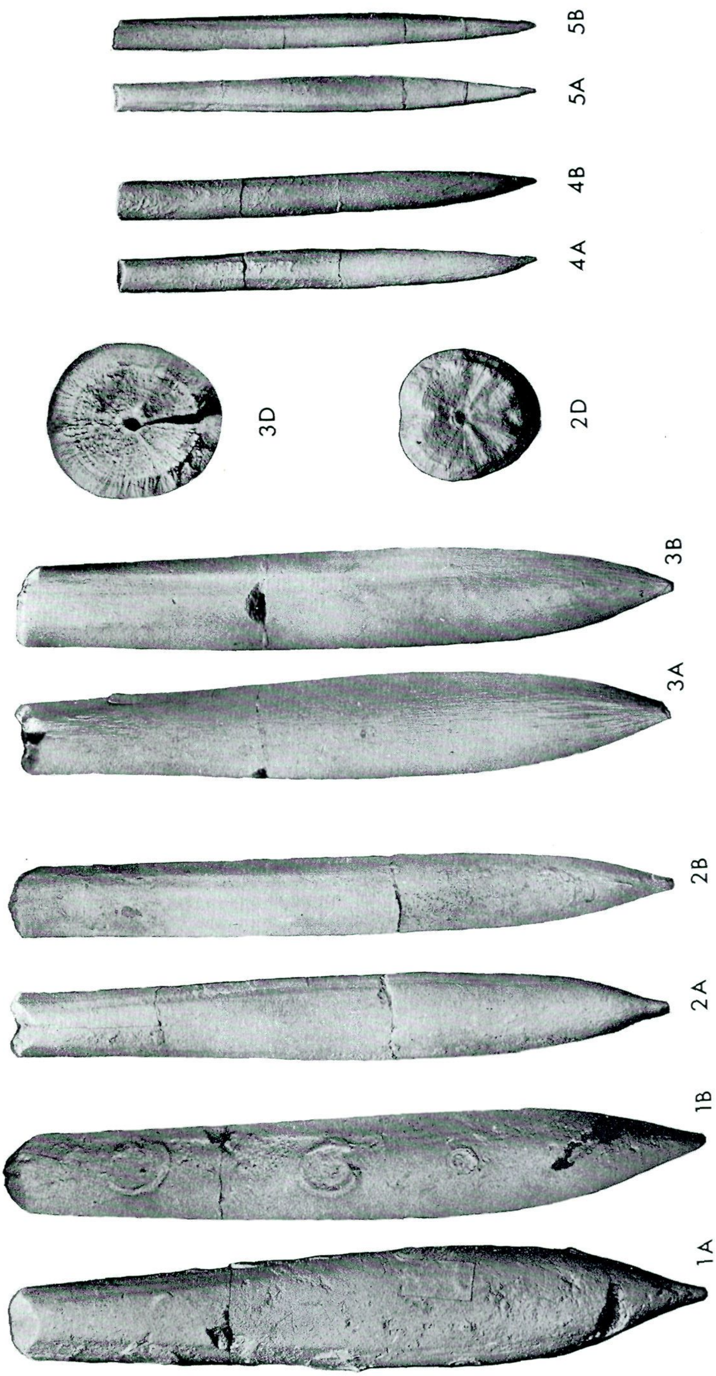

5B
5A
4B
4A
3D
2D
3B
3A
2B
2A
1B
1A

Plate 3

All figures are of natural size unless otherwise indicated. Specimens are coated with ammonium chloride.

Figs. 1–6. *Actinocamax plenus* (Blainville, 1825) from the Plenus Marls of the Betchworth Limeworks. A: Dorsal view. – B: Lateral view. – C: Ventral view. – D: View of the adoral part of the guard. 1: Zb 1913. – 2: B 76720.– 3: B 76721. – 4: Zb 1969. – 5: Zb 1912. – 6: Zb 1787.

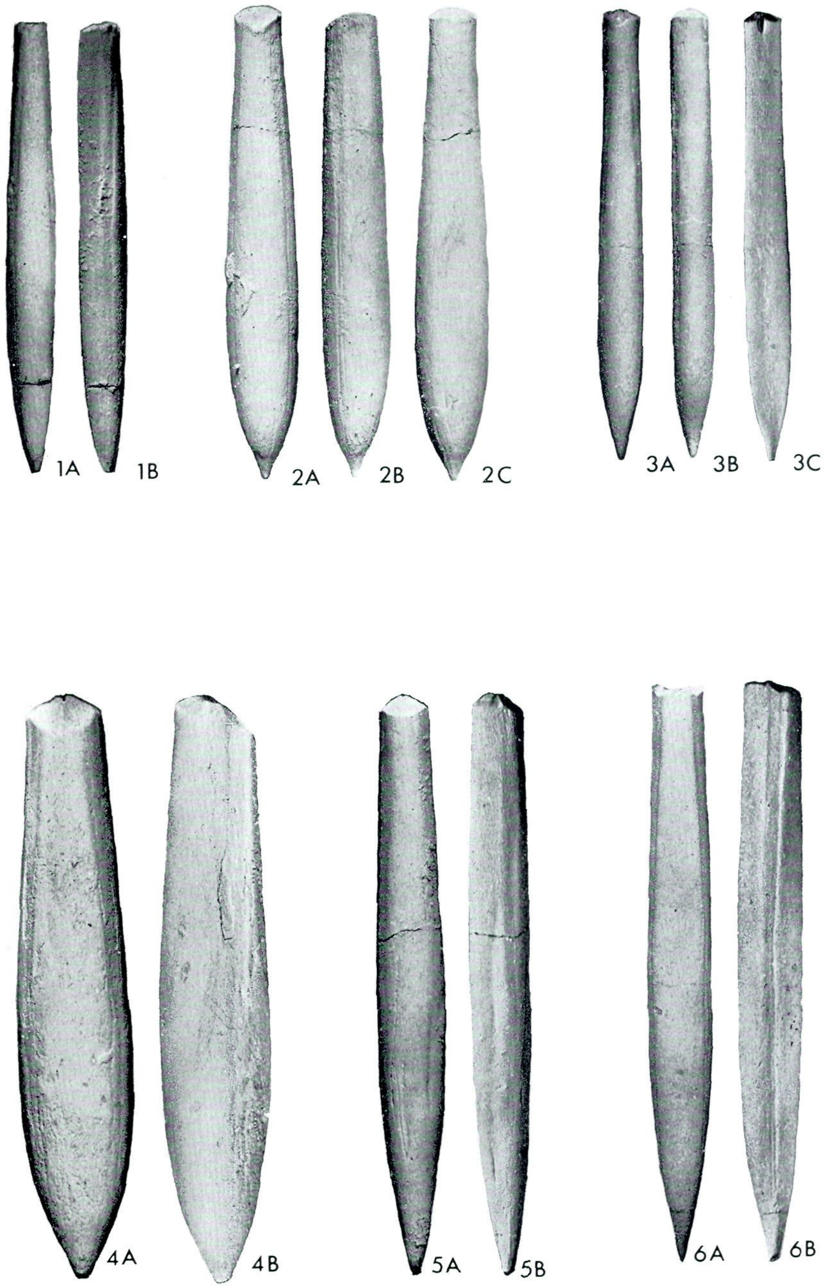
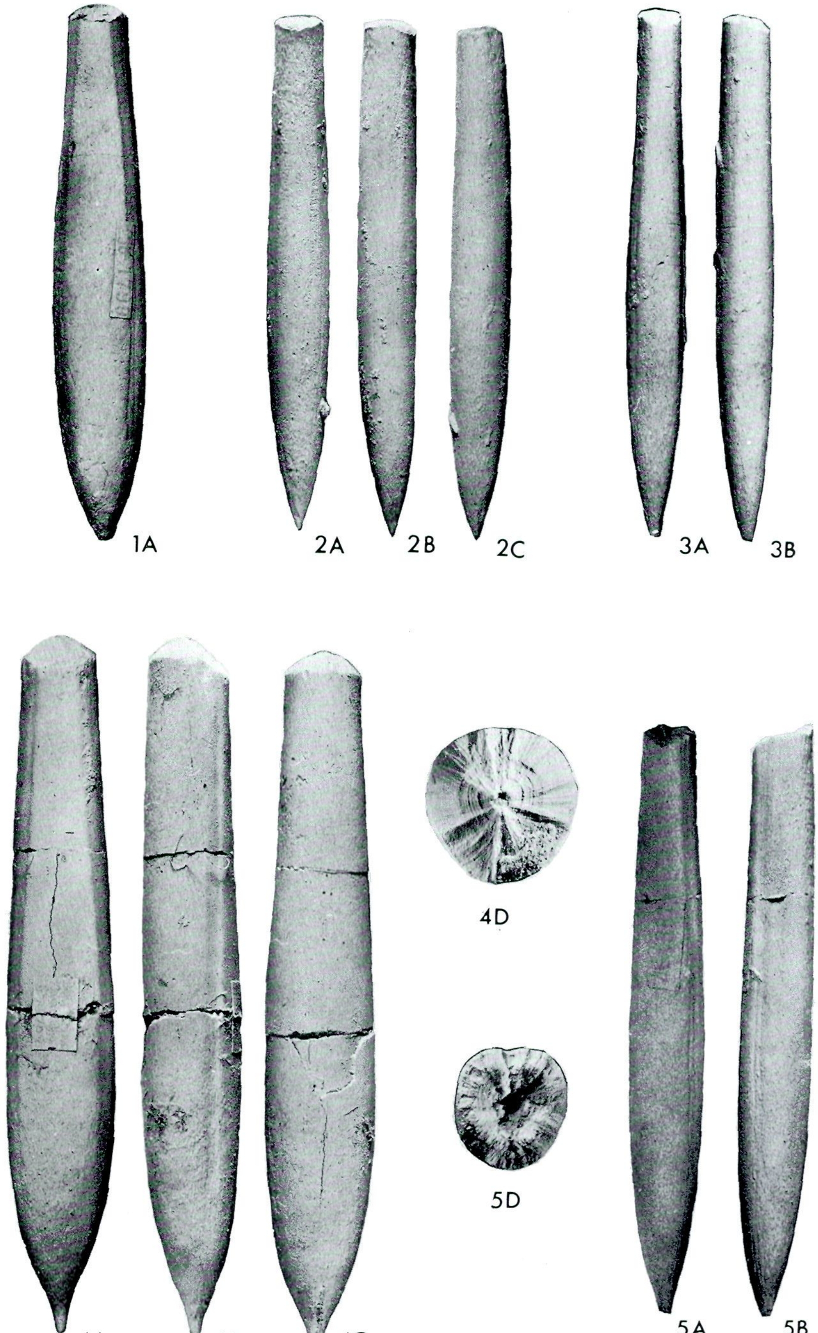

1A
1B
2A
2B
2C
3A
3B
3C
4A
4B
5A
5B
6A
6B

Plate 4

All figures are of natural size unless otherwise indicated. Specimens are coated with ammonium chloride.

Figs. 1–5. *Actinocamax plenus* (Blainville, 1825) from the Plenus Marls of the Betchworth Limeworks. A: Dorsal view. – B: Lateral view. – C: Ventral view. – D: View of the adoral part of the guard. 1: Zb 1799. – 2: B 76714. – 3: Zb 1855. – 4: B 76709. – 5: Zb 1887. Figs 4D and 5D, × 2.


1A
2A
2B
2C
3A
3B
4A
4B
4C
4D
5D
5A
5B

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