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ACTA UNIVERSITATIS STOCKHOLMIENSIS

STOCKHOLM CONTRIBUTIONS IN GEOLOGY

VOL. IX:4

BIOMETRIC STUDY OF ACTINOCAMAX VERUS S.L. FROM THE UPPER CRETACEOUS OF THE RUSSIAN PLATFORM

By

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Distributor ALMQVIST & WIKSELL *Gamla Brogat. 26, Stockholm*

4. Biometric study of Actinocamax verus s.l. from the Upper Cretaceous of the Russian Platform

By

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Abstract. Material of the belemnite species *Actinocamax verus* MILLER s.l. (237 specimens) from 9 localities in the Coniacian, Santonian, and Campanian of the Russian Platform are analysed biometrically by methods of univariate and multivariate statistical analysis. The results of the investigation show the probable existence of univariate and multivariate chronoclines; strong morphologic differences between samples would seem in part to be due to chronomorphologic differentiation and in part to postmortal mechanical sorting. The effects of postmortal sorting are brought out by an investigation on the homogeneity of covariance matrices of the samples in which it is demonstrated that considerable differences occur; they are also underlined by noteworthy heterogeneity in the correlation coefficients for some of the variables. The generalized distance study, based on four variables and six samples, produces a distorted topologic model. This is interpreted as being due to the fact the six covariance matrices obtained

from these samples, although homogeneous with respect to the test criterion, are still not truly equal, and also to the possibility that the three-dimensional representation of the model is inadequate. A trial septivariate generalized distance shows that little is won by increasing the dimensionality of the study above four variables. Two-dimensional generalized distances for two groupings of the four key variables are also given. A discriminant function analysis for three groupings is given (the groups being based on the results of the generalized distance study). Univariate and multivariate coefficients of variation are presented as well as coefficients of scatter. A septivariate principal component study permits tentative conclusions on the size and shape variation of the material. Seven factors were extracted of which the first accounts for 72 % of the total variation, the second for 13 % and the third for 10 %. Quadrivariate principal component analyses are also presented. The correlation coefficients for each sample are treated graphically by the method of morphological integration, the groupings made being decided by the results of the principal component analysis. The biometric study is made on the entire material of *Actinocamax verus* MILLER s. l. in order to avoid subjective selection of observations. As indicated in the paleontological section, however, it would seem possible on biostratigraphic and paleontologic grounds to be able to bring about subspecific taxonomic differentiation of the material and this is to a considerable extent supported by the morphologic biometric analysis.

Аннотация. Были подвергнуты биометрическому изучению методами одно- и многовариантного статистического анализов мелкие актинокамаксы, принадлежащие группам *Actinocamax verus fragilis* ARKHANGELSKI и *A. verus laevigatus* ARKHANGELSKI и происходящие из ряда обнажений коньякских, сантонских и нижнекампанских отложений Русской платформы.

Результаты исследования показывают, что, по-видимому, существуют одно- и многовариантные хроноклины. Значительные морфологические различия между образцами частично могут быть объяснены наличием хрономорфологических различий и частично влиянием посмертной сортировки ростров. Эффект посмертной сортировки отчетливо выявляется при изучении однородности ковариантных матриц образцов, обладающих большими различиями. Этот же эффект подчеркивается в случае заметной неоднородности коэффициентов корреляции некоторых переменных.

Изучение расстояния Маханалобиса, основанное на четырех переменных и шести образцах, позволило построить модель искажений. Предполагается, что искажения обусловлены, во-первых, тем, что шесть ковариантных матриц, хотя и однородные в пре-

делах определенных границ, все же довольно различны и, во-вторых, возможностью того, что при несовместимости переменных трехмерных пространственных изображений оказывается недостаточно.

Изучение дискриминантных функций было проведено для пар и для трех групп, основанных на расстоянии Маханалобиса. Вычислены одно- и многовариантные коэффициенты изменчивости, а также коэффициенты рассеивания. Изучение основных компонентов показало, что замеры величины альвеолярного излома не образуют приемлемых значащих сочетаний с замерами других величин ростра. Это же было показано и на других стадиях работы.

Коэффициенты корреляции для каждого образца были изображены графически посредством метода морфологической интерпретации; группирование проводилось по результатам основного компонентного анализа. Для сравнения приводятся два ряда бивариантных обобщенных расстояния, основанных на двух группах переменных.

Статистическое изучение *Actinocamax verus* MILLER s. l. проводилось для того, чтобы исключить субъективность в выборе наблюдений. Однако, как показано в палеонтологическом разделе работы, представляется возможным на основании биостратиграфических и палеонтологических данных выделить в пределах исследованного вида подвиды. Этот результат частично подтверждается данными морфобиометрического анализа.

INTRODUCTION

The work forming the basis of this report was initiated during a visit by R. A. R. in Moscow in the winter of 1960—1961. It arose out of a discussion concerning the possibility of using belemnites in a more detailed subdivision of the Upper Cretaceous of the Russian Platform. D. P. N. had made a collection of small *Actinocamax* from various levels in the Coniacian, Santonian, and Campanian and it was decided to use this material to test the hypotheses arrived at. The measurements were made in collaboration, about half being done by R. A. R. and about half by D. P. N. The main collecting was done in 1954, but other collections were made in 1949 and at other periods.

The authors wish to thank Professor A. A. BOGDANOV, Head of the Department of Historical Geology at the University of Moscow, for permitting use of the facilities and collections of his institute and Professor I. R. HESSLAND, Head of the Department of Geology at the University of Stockholm, for advice, encouragement and facilities for the preparation and publication of the results.

Some of the routine computational work was done by the class in Paleontologic Biometry at the University of Stockholm for 1961. The figures and model were made by Mr. L. ZACKRISSON of the Department of Geology of the University of Stockholm. Much appreciated assistance was rendered by Miss G. N. YUREL of the Department of Historical Geology of the University of Moscow.

For gifts of literature and help of other kinds we are indebted to Dr. R. BLACKITH, London, Dr. J. HANCOCK, London, Dr. P. JOLICOEUR, Montreal, and Mr. C. W. WRIGHT, London.

Financial assistance for the publication costs was generously given by "Kungafonden" and The Swedish Natural Science Research Council.

Simple computations were performed on a FRIDÉN desk calculator (square-root model) and Åtvidaberg FACIT desk calculators; the septivariate computations were made on and all quadrivariate calculations were checked on the computers BESK (Binary Electronic Sequential Calculator) and FACIT of the Swedish Board for Computing Machinery (Matematikmaskinnämnden), Stockholm. The measured material is kept in the collections of the Department of Historical Geology of the University of Moscow, Moscow V-234. The biometric section was written by R. A. R. and the paleontologic section contributed by D. P. N.

PROVENANCE OF THE MATERIAL

The material here treated is derived from the following localities: (1) Djurun, Ural-Emba region — 5490-1 (Lower Campanian; Cmp_1), (2) Don River (Boguchar) — 931-1b (Lower Campanian; Cmp_1), (3) Ulianovsk — 359 (Santonian; Snt), (4) Don River (Boguchar) — 935-1b (Lower Campanian; Cmp_1), (5) Lgov — 146-2 (Santonian; Snt), (6) Don River (Kazanskaia) — 922-1b (Lower Campanian; Cmp_1), (7) River Sura — 8012 (Upper Coniacian; Cn_2), (8) Don River (Kazanskaia) — 917b (Lower Campanian; Cmp_1), (9) River Volga — 5322 (Lower Coniacian; Cn_1).

The numbers 1—9 are used hereinafter to designate the nine occurrences treated in this paper. The numbers following the geographic names refer to the catalog numbers in the collection of the University of Moscow. The letters after the stage names refer to the standard designations for the Cretaceous in the Stratigraphic Code of the Soviet Union; the use of these is shown, for example, in NAIDIN (1960, table facing p. 44). For a detailed discussion of the bases of the stratigraphic determinations reference is made to NAIDIN (1960).

A highly condensed account of the stratigraphy of the Coniacian, Santonian and Lower Campanian of the central part of the Upper Cretaceous development of the Russian Platform (Volga region, Don Basin), the region from which the belemnites were obtained, is presented below.

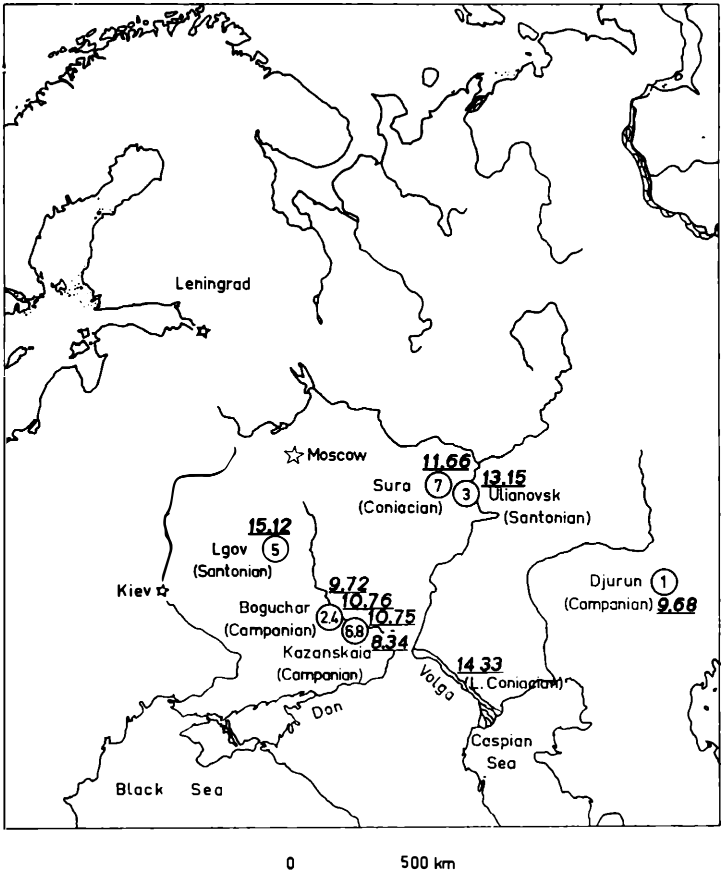

Fig. 1. Map of the European part of the U. S. S. R. showing the localities, and their respective ages, from which the material of *Actinocamax* was collected.
The underlined numbers refer to values obtained in the discriminant function analysis.

Upper Turonian. The Upper Turonian of the area under review is built up of sandstones, chalks and limestones containing *Inoceramus lamarcki* PARKINSON and related forms.

Lower Coniacian. The lithological development of the Lower Coniacian is similar to the foregoing; it contains locally abundant occurrences of *Inoceramus wandereri* ANDERT, *I. deformis* MEEK, *I. kleini* MÜLLER, *Micraster cortestudinarium* GOLDFUSS, to name a few of the important forms. In the Volga region, from which sample 9 was collected (5322), the beds do not contain well preserved macrofossils.

Upper Coniacian. This is well developed in the unbroken sequences of the Donbass and also in the Ulianovsk district of the Volga region. In the latter area, from which sample 7 (8012) is derived, the Upper Coniacian consists of marls containing *Inoceramus involutus* SOWERBY, *I. percostatus* MÜLLER, *Actinocamax lundgreni* STOLLEY and many small *Actinocamax.*

Santonian. There is generally a clear transition between Upper Coniacian and Santonian to be observed in sections. In the Volga region the Santonian rocks consists of marls and siliceous sediments — opokas, kieselguhr, and silicified marls. In the more westerly parts of the Russian Platform marls dominate. Characteristic belemnites of the Volgan Santonian are *Belemnitella propinqua* MOBERG, *B. praecursor* STOLLEY s. l., *Actinocamax verus fragilis* ARKHANGELSKI, and for the lower part of the stage, *Inoceramus cardissoides* GOLDFUSS.

Lower Campanian. The lower part of the Lower Campanian (the so-called "*Pteria* beds") lie transgressively on the various levels of the lower part of the Upper Cretaceous. In the Volgan Region and the Don Basin the "*Pteria* beds" are represented by series of marls or siliceous rocks (for example, opokas) for which the most characteristic fossil is *Oxytoma* (*Pteria*) *tenuicostata* RÖMER. Considerably less common is *Belemnitella praecursor* STOLLEY s. l. and less common again are large forms related to *Actinocamax grossouvrei* JANET. Small rostra of *Actinocamax verus laevigatus* ARKHANGELSKI may be locally abundant. Material referable here is described from localities 2 (931-1b), 4 (935-1b), 6 (922-1b), 8 (917b), collected from the valley of the River Don in the Voronezh and Rostov areas. In the south-eastern outskirts of the Russian Platform in the Ural-Emba region (Djurun and other areas) the "*Pteria* beds" are developed as sandstones, in which the small rostra of a form allied to *Actinocamax verus laevigatus* ARKHANGELSKI are found, as well as abundant rostra of *Belemnitella praecursor* STOLLEY and large *Actinocamax,* as yet unstudied.

SHORT PALEONTOLOGIC CHARACTERIZATION OF *ACTINOCAMAX VERUS* s. l.

In the following section short paleontological descriptions of the small *Actinocamax* of the Upper Cretaceous of the Russian Platform are given, of which some have also been treated in the biometric study.

The small *Actinocamax* forms of the Platform may be separated into two groups with distinct stratigraphic developments. The first group comprises forms close to *Actinocamax verus fragilis* ARKHANGELSKI and occurring in the Coniacian and Santonian; representatives of this group do also occur in the "*Pteria* beds" of the lower part of the Lower Campanian, but such appearances are very rare. The second lot is constituted by forms grouping around *Actinocamax verus laevigatus* ARKHANGELSKI and restricted to the "*Pteria* beds" of the Lower Campanian.

The rostral length of small *Actinocamax* lies mostly within the range 2.8 to 3.5

cm (rarely up to 5.5 cm), whereas the ranges for the rostral lengths of large species of *Actinocamax* lie around 6.0—8.0 cm and 1.1—1.2 cm. The rostra have many shapes; they may be almost cylindrical, spindle-shaped, fusiform, or club-shaped. The dorsolateral double-furrows are well developed. In many forms the rostral surface is covered with a fine, transverse texture of wrinkles and granulations.

The anterior part of the rostrum is provided with the high, conical alveolar fracture. The fracture line, or scar, may be symmetric or asymmetric; in the former case the dorsal side is more deeply incised than the ventral. The scar may be set off sharply from the surface of the rostrum or may merge gradually into the latter.

THE GROUP OF *ACTINOCAMAX VERUS FRAGILIS* ARKHANGELSKI

Rostrum of variable shape. The majority of specimens display the texture here termed that of "shagreen leather". Alveolar scar set off sharply from the rostral surface.

Actinocamax verus fragilis ARKHANGELSKI
Fig. 2, *1—7*, *10*, *11*, *15*, *16*

DESCRIPTION. — The granulation of the surface of the rostrum is readily discernible. As a general estimation of the rostral length 3.5 cm may be taken. The shape of the rostrum and the extent of the asymmetry of the alveolar scar display appreciable variability. Most specimens are spindle-shaped, thickening somewhat at the sides in the anterior part of the rostrum; the alveolar scar is strongly asymmetrical, its dorsal height ranging around 4—9 mm and its median height ranging around 6—7 mm (Fig. 2, *1*, *5*; cf. ARKHANGELSKI, 1912, pl. 9, figs. 16, 17).

REMARKS. — The subspecies here under discussion is distributed in the Coniacian and the Santonian. Sample 5 (156-2) from the Santonian of Lgov belongs here as well as sample 9 (5322) from the Lower Coniacian of the Volga. In the Santonian, forms are also encountered which have a strongly swollen posterior third (Fig. 2, *10*, *11*). These are particularly common in the Ulianovsk area. Part of the material comprising sample 3 (359) from the Santonian of Ulianovsk has this kind of rostrum. In the Santonian, and also very rarely in the lower part of the Lower Campanian, forms may occur which are slightly differently built. They may be almost cylindrical to faintly cigar-shaped with a relatively high, weakly asymmetrical alveolar scar (Fig. 2, *6*, *7*, *16*). Short rostra are encountered only very occasionally (Fig. 2, *15*). Finally, in the Upper Coniacian beds of the River Sura spindle-shaped rostra occur, the alveolar scars of which are weakly asymmetric, and whose rostral tip

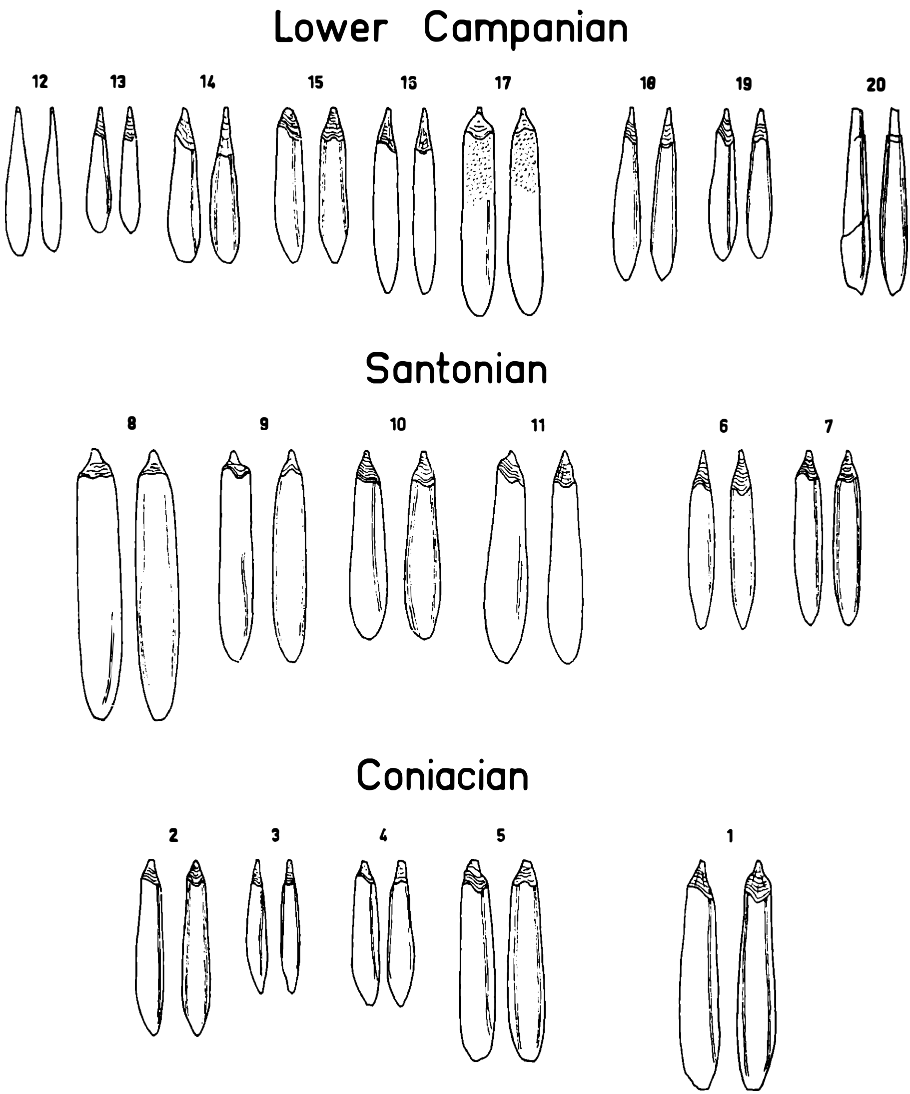

Fig. 2.

1—7, 10, 11, 15, 16. Actinocamax verus fragilis ARKHANGELSKI. *1,* Lower Coniacian of the River Volga, near Saratov, N 5322-1; *2—4*, Upper Coniacian of the River Sura, N 8012, N 382; *5*, Upper Coniacian of the River Volga, near Saratov, N 5365; *6*, *7*, Santonian of the River Volga, near Saratov, N 5312, N 5323; *10*, *11*, Santonian, Ulianovsk, N 359, N 8027; *15*, *16*, "*Pteria* beds", lower part of Lower Campanian, River Don, near Kazanskaia (*15* — N 922-1E), and near Boguchar (*16* — N 935-1E).

8, 9, 17. Actinocamax verus verus MILLER. *8*, Upper Santonian, Crimea, N 1001; *9*, Santonian, Donbass, N 826; *17*, "*Pteria* Beds", lower part of the Lower Campanian, River Don near Boguchar, N 935-1b.

is displaced dorsally. (Fig. 2, *2*, *3*, and *4*). The biometric variation of this material of Upper Coniacian age (8012) is studied in this paper (sample 7).

Actinocamax verus verus MILLER
Fig. 2, *8*, *9*, *17*

DESCRIPTION. — Usually provided with the shagreen-leather texture in the anterior part of the rostrum. The rostra are relatively large compared with those of other "small actinocamacids". The rostra are almost cylindrical in shape to weakly spindle-shaped but anteriorly they are somewhat compressed from the sides. The alveolar scar is relatively low (3—6 mm); it is symmetrically developed.

REMARKS. — This subspecies is occasionally met with in the Crimean Santonian (Fig. 2, *8*) and in the Donbass (Fig. 2, *9*), and also in the "*Pteria* beds" of the Lower Campanian of the basin of the Don (Fig. 2, *17*). Twelve specimens of the subspecies are known from this latter region (samples 2, 4, 6).

THE GROUP OF *ACTINOCAMAX VERUS LAEVIGATUS* ARKHANGELSKI

Rostra club-shaped; there is a sharply marked inflation in the posterior third or fourth of the rostrum. A very characteristic feature of the group is the flattening of the sides, particularly in the anterior part of the rostrum. The alveolar scar is relatively high and usually symmetrically developed, rarely asymmetric. A further characteristic feature is the tendency for the scar zone to merge into the rostral surface.

Actinocamax verus laevigatus ARKHANGELSKI
Fig. 2, *12—14*

DESCRIPTION. — On the whole the rostrum of this subspecies tends to be smaller than that of other subspecies of *A. verus*; we note that the average rostral length for the material of the species from locality 4 (935-1b) is about 2.9 cm and for 78 rostra from locality 2 (931-1b) the length is about 2.85 cm. The clublike inflation of the rostrum occurs at about the posterior third of the

12—14. *Actinocamax verus laevigatus* ARKHANGELSKI. All specimens from the "*Pteria* Beds", River Don near Boguchar, N 931-1b, N 935 1b.

18—19. *Actinocamax verus laevigatiformis* NAIDIN subsp. nov. From the "*Pteria* Beds", Djurun, in the Ural-Emba region, N 5490-1.

20. *Actinocamax verus pseudolaevigatus* NAIDIN subsp. nov. From the "*Pteria* Beds", River Synja, Western Siberia, N 901.

[The numbers of the figured specimens in the collection at Moscow University are: *1* (9), *2*, *3*, *4* (31), *5* (5), *6*, *7* (54), *8* (2), *9* (4), *10*, *11* (24), *12* (1), *13*, *14* (316), *15* (20), *16* (11), *17* (12), *18*, *19* (34), *20* (2).]

All figures natural size.

length. The sides are distinctly flattened. The alveolar scar is relatively high, the height of the alveolar cone ranging around 6—7 mm, very occasionally, however, attaining 11 mm; it is weakly asymmetric.

REMARKS. — The rostra of this subspecies are locally very common in the "*Pteria* beds" of the Don Basin and the Volgan region, where they predominate greatly amongst the small *Actinocamax.*

Actinocamax verus laevigatiformis NAIDIN subsp. nov.
Fig. 2, *18, 19*

DESCRIPTION. — The rostra of this form seem to be relatively more elongated than those of the other subspecies. On the basis of 12 specimens from the Djurun locality (5490-1b) the average rostral length lies around 3.2 cm. The flattening of the rostral sides is less apparent than in *A. v. laevigatus.* The alveolar scar, which is asymmetrical, is relatively high, ranging around 6—8 mm in height.

HOLOTYPE. — N 5490—1 E/8, Djurun, Ural-Emba Region, Fig. 2, *18.*

AGE. — The rostra of this form occur in the "*Pteria* beds" of the Ural-Emba area.

Actinocamax verus pseudolaevigatus NAIDIN subsp. nov.
Fig. 2, *20*

DESCRIPTION. — These strongly club-shaped rostra have an average rostral length of around 4.0 cm. The anterior part of the rostrum is very tapered (roughly in two phases). The sides are feebly flattened and the dorsal side is narrowed. The tip of the rostrum is usually slightly displaced in a dorsal direction. The alveolar scar passes imperceptibly into the surface of the rostrum.

HOLOTYPE. — N 90/1, River Synja, Western Siberia, Fig. 2, *20.*

AGE. — This subspecies occurs in the basin of the River Synja, a tributary of the River Ob, where it is found together with *Oxytoma tenuicostata* RÖMER and *Belemnitella praecursor* STOLLEY s. l. No material of the form here described is treated in the statistical section of the present paper.

GENERAL REMARKS

It is here pointed out that the subspecific designations employed in the foregoing may well have definite zoologic meaning inasmuch as the subspecific category is generally accepted to be a geographically defined local population exhibiting some form of taxonomic differentiation from the other subspecific entities of the species, which implies that no more than one breeding population of a subspecies can occupy a given geographic or ecologic space. In the present study the two groups of "*A. v. fragilis*" and "*A. v. laevigatus*" probably represent genuine zoologic subspecies in the sense peculiar to Paleontology, notably, that they do not occupy the same time space and are therefore in effect chronologic races. The fact that statistically significant differences do occur between these two groups offers support for this hypothesis.

ARKHANGELSKI (1912, p. 597) claimed that the small *Actinocamax* of the Santonian of the European part of the U.S.S.R. differ from the development of *Actinocamax verus* MILLER s. l. in contemporaneous deposits of Europe according to the descriptions of MILLER (1823, pp. 64—67, pl. 9, figs. 17—18), SCHLÜTER (1876—1877, p. 191, pl. 42, figs. 9—15), MOBERG (1885, p. 46, pl. 4, figs. 15—26), and STOLLEY (1897, pp. 77, 78, pl. 4, figs. 2—5) as well as other authors. Our observations would appear to corroborate this inference of ARKHANGELSKI. However, in the material from the Russian Platform, forms are occasionally encountered which fall outside of the range of *A. v. fragilis* and which would seem to be referable to *A. v. verus*. Such forms are met with in the Santonian and Lower Campanian beds of the southern peripheral extent of the Cretaceous of the Platform (Western Ukraine, Basin of the Don), and in the Crimea. On the other hand, in Europe proper, where the principal distribution of *A. v. verus* occurs, typical *A. v. fragilis* would seem to be scarce (MOBERG, 1885, pl. 4, fig. 22 (?), BIRKELUND, 1957, p. 24). Apparently, *A. v. verus* MILLER and *A. v. fragilis* ARKHANGELSKI are to be regarded as geographic subspecies.

Representatives of the "*laevigatus*" group occur only in the "*Pteria* beds" of the Lower Campanian. These beds are widely distributed and the material studied in the present connexion comes from relatively widely separated occurrences. There would therefore appear to be a possibility that isolated geographic subspecies could have developed: *A. v. laevigatus* in the Volga region and the Don Basin; *A. v. laevigatiformis* in the south-eastern reaches of the Platform; *A. v. pseudolaevigata* in the boreal paleogeographic province.

DISCUSSION OF THE BIOMETRIC METHODS USED

In addition to the standard methods of univariate and bivariate analysis, certain methods of multivariate analysis have been employed in this paper. References are given to standard textbooks and papers in which these topics are given expositionary discussion. The samples were tested for homogeneity of correlation coefficients (RAO, 1952) and homogeneity of covariance matrices by the multivariate analog of the BARTLETT test (ANDERSON, 1958; REYMENT, 1960 a). A single classification multivariate analysis of dispersion (manova) (RAO, 1948) was made and also a sequence of HOTELLING T^2-tests (ANDERSON, 1958). MAHALANOBIS' generalized distances between samples with homogeneous covariance matrices were calculated (RAO, 1949a, 1952). A discriminant function between Santonian and Campanian samples and for $\pi > 2$ were calculated (ANDERSON, 1958). Generalized coefficients of variation (REYMENT, 1960a), univariate coefficients of variation and Frischian coefficients of scatter (REYMENT, 1960a) were computed for each sample. Principal component analyses of several large samples were made (ANDERSON, 1958).

Common symbols used are $\mathbf{\Sigma}$, $\mathbf{S}$ = covariance matrix, μ, $\bar{\mathbf{x}}$ = mean vector, σ, s = standard deviation, μ, $\bar{x}$ = mean, $\mathbf{P}$, $\mathbf{R}$ = correlation matrix, r = correlation coefficient, V = coefficient of variation. In most cases Greek letters denote population quantities. [Letters printed in boldface capitals denote matrices, those printed in boldface lower case letters denote vectors, and those printed in italics are scalars. All measurements in cm.]

A special study of the observed heterogeneity of covariance matrices has been published by R. A. R. (REYMENT, 1962). The concept of "morphological integration", as presented by OLSON and MILLER (1958) is employed; this method requires the correlation coefficients between pairs of variables.

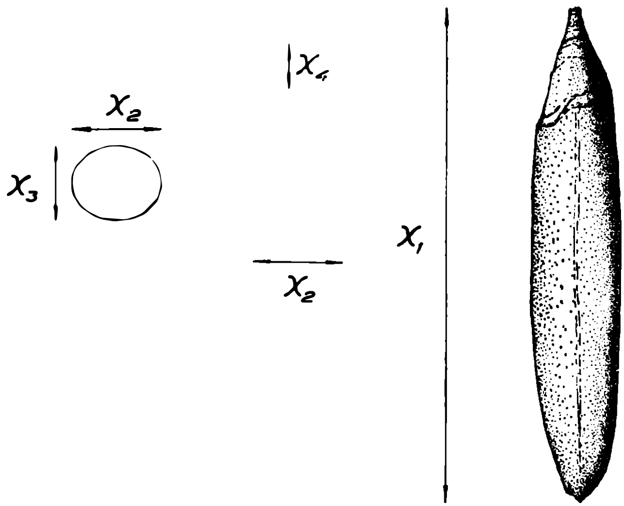

Fig. 3. The four principal characters measured on the rostra of *Actinocamax verus* MILLER s. l.

BASIC STATISTICAL DATA

The data are presented separately for each of the samples 1—8. The following 7 characters were measured on each belemnite rostrum: length of rostrum (x_1), maximum breadth of rostrum (x_2), maximum width of rostrum in the plane at right angles to that containing the foregoing measurement (x_3), asymmetry of alveolar scar (x_4), distance of site of maximum inflation of rostrum from rostral tip (x_5), distance of upper side of alveolar scar from alveolar scar tip (x_6), distance of lower side of alveolar scar from alveolar scar tip (x_7). Obviously x_4 is dependent on x_6 and x_7 and for most of the multivariate calculations the latter two measurements were excluded. Owing to the difficulty of obtaining accurate observations on x_5 it was excluded from almost all advanced calculations. The sites of the four principal measurements x_1, x_2, x_3, x_4, are shown in Fig. 3. Dimension x_1 may be subject to error owing to attrition of the rostrum but as disclosed by its coefficient of variation this is negligible in the present material.

Sample 1

Locality. — Djurun, 5490-1.

Age. — Lower Campanian: Cmp_1.

Number of specimens. — 24.

Dimension	$\bar{x}$	s	V	Observed range
x_1	3.160 (3.050—3.270)	0.2557 (0.199—0.359)	7.92 ± 1.17	2.75—3.80
x_2	0.515 (0.491—0.539)	0.0557 (0.043—0.078)	10.62 ± 1.57	0.40—0.66
x_3	0.479 (0.462—0.496)	0.0387 (0.030—0.054)	8.02 ± 1.18	0.39—0.55
x_4	0.232 (0.162—0.302)	0.1584 (0.123—0.222)	66.90 ± 8.40	0.03—0.67
x_5	1.311 (1.187—1.435)	0.2566 (0.205—0.368)	19.57 ± 3.39	0.72—1.52
x_6	0.618 (0.564—0.672)	0.1241 (0.096—0.174)	20.08 ± 2.90	0.38—0.95
x_7	0.387 (0.331—0.443)	0.1303 (0.101—0.183)	33.67 ± 4.86	0.01—0.63

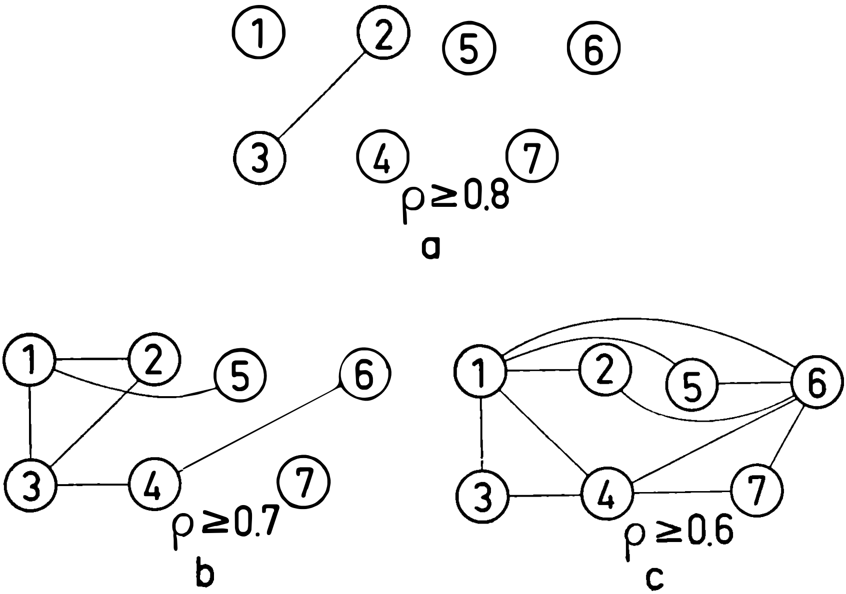

Fig. 4. Levels of correlation for the seven variates; *a*, $\varrho \geq 0.8$; *b*, $\varrho \geq 0.7$; *c*, $\varrho \geq 0.6$.

Sample mean vector

$$\bar{\mathbf{x}} = \begin{bmatrix} 3.160 \\ 0.515 \\ 0.479 \\ 0.232 \end{bmatrix}.$$

Sample covariance matrix

$$23\,\mathbf{S} = \begin{bmatrix} 1.5039 & 0.1831 & 0.1417 & 0.3939 \\ & 0.0719 & 0.0382 & -0.0168 \\ & & 0.0355 & 0.0394 \\ & & & 0.5778 \end{bmatrix}.$$

Sample correlation matrix

$$\mathbf{R} = \begin{bmatrix} 1.000 & 0.556 & 0.613 & 0.423 & 0.541 & 0.478 & 0.108 \\ & 1.000 & 0.756 & -0.082 & -0.154 & 0.036 & 0.096 \\ & & 1.000 & 0.275 & -0.070 & 0.275 & 0.004 \\ & & & 1.000 & -0.175 & -0.631 & -0.453 \\ & & & & 1.000 & 0.403 & -0.175 \\ & & & & & 1.000 & 0.403 \\ & & & & & & 1.000 \end{bmatrix}.$$

In this case, and all ensuing, the correlation matrix in the upper left hand corner is that which is used in the subsequent quadrivariate multivariate calculations.

In the diagrams in Fig. 4 the so-called degree of morphological integration on the basis of correlation coefficients is shown. The diagrams indicate the levels of correlation between variate pairs (see OLSON and MILLER, 1958; TERENTIEV, 1960).

For the purposes of the construction of these diagrams the variates are considered to comprise two functional groups. The first of these consists of the four dimensions x_1, x_2, x_3, x_5, which are concerned with the size dimensions of the belemnite rostrum. The second group consists of the three dimensions x_4, x_6, x_7, which are concerned with the asymmetry of the alveolar scar.

Histograms of the variates show that x_2 and x_3 are good approximations to the normal distribution, while x_1 has a flat-topped distribution and x_4 is only a fair approximation to the normal distribution.

SAMPLE 2

LOCALITY. — Boguchar, 931-1b.

AGE. — Lower Campanian: Cmp_1.

NUMBER OF SPECIMENS. — 52.

Dimension	$\bar{x}$	s	V	Observed range
x_1	2.799 (2.739—2.859)	0.2117 (0.176—0.261)	7.49 ± 0.73	2.07—3.48
x_2	0.523 (0.503—0.543)	0.0714 (0.060—0.088)	13.65 ± 1.34	0.37—0.69
x_3	0.479 (0.460—0.498)	0.0686 (0.057—0.084)	14.32 ± 1.41	0.35—0.66
x_4	0.235 (0.209—0.261)	0.0927 (0.077—0.114)	39.44 ± 3.87	0.00—0.43
x_5	0.823 (0.763—0.883)	0.2116 (0.176—0.261)	25.71 ± 2.52	0.42—1.31
x_6	0.668 (0.633—0.703)	0.1249 (0.104—0.154)	18.70 ± 1.83	0.39—0.99
x_7	0.433 (0.403—0.463)	0.1072 (0.089—0.132)	24.76 ± 2.43	0.22—0.70

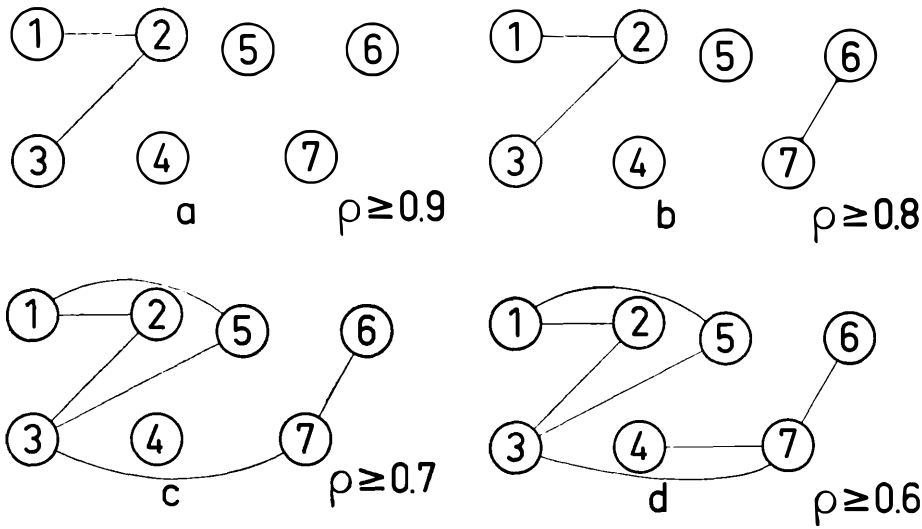

Fig. 5. Levels of correlation for the seven variates; *a*, $\varrho \geq 0.9$; *b*, $\varrho \geq 0.8$; *c*, $\varrho \geq 0.7$; *d*, $\varrho \geq 0.6$.

The sample mean vector

$$\bar{\mathbf{x}} = \begin{bmatrix} 2.799 \\ 0.523 \\ 0.479 \\ 0.235 \end{bmatrix}.$$

The sample covariance matrix

$$51\,\mathbf{S} = \begin{bmatrix} 2.2833 & 1.1335 & 0.3419 & 0.4771 \\ & 0.2626 & 0.2326 & 0.0025 \\ & & 0.2386 & 0.0358 \\ & & & 0.4399 \end{bmatrix}.$$

The sample correlation matrix

$$\mathbf{R} = \begin{bmatrix} 1.000 & 0.933 & 0.296 & 0.300 & 0.584 & 0.286 & 0.419 \\ & 1.000 & 0.930 & 0.074 & 0.200 & 0.200 & 0.074 \\ & & 1.000 & 0.111 & 0.568 & 0.001 & -0.583 \\ & & & 1.000 & 0.160 & 0.509 & -0.214 \\ & & & & 1.000 & 0.296 & 0.362 \\ & & & & & 1.000 & 0.713 \\ & & & & & & 1.000 \end{bmatrix}.$$

The pattern of integration between variables is shown in Fig 5 (cf. p. 161).

Histograms of the variates x_1, x_2, x_3, x_4 show all are reasonable approximations to the normal distribution, even if x_2 and x_3 tend to be peaked.

Sample 3

Locality. — Ulianovsk, 359.

Age. — Santonian: Snt.

Number of specimens. — 17.

Dimension	$\bar{x}$	s	V	Observed range
x_1	3.479 (3.216—3.742)	0.4960 (0.3811—0.7780)	14.26 ± 2.45	2.32—4.28
x_2	0.613 (0.545—0.681)	0.1288 (0.099—0.202)	21.01 ± 3.60	0.32—0.79
x_3	0.588 (0.524—0.652)	0.1204 (0.093—0.189)	20.48 ± 3.51	0.30—0.77
x_4	0.282 (0.225—0.339)	0.1082 (0.083—0.169)	38.37 ± 6.58	0.06—0.44
x_5	1.324 (1.181—1.467)	0.2691 (0.200—0.410)	20.32 ± 3.49	0.92—1.73
x_6	0.646 (0.470—0.822)	0.3314 (0.247—0.504)	51.30 ± 8.80	0.25—1.08
x_7	0.364 (0.299—0.429)	0.1229 (0.092—0.187)	33.79 ± 5.79	0.10—0.72

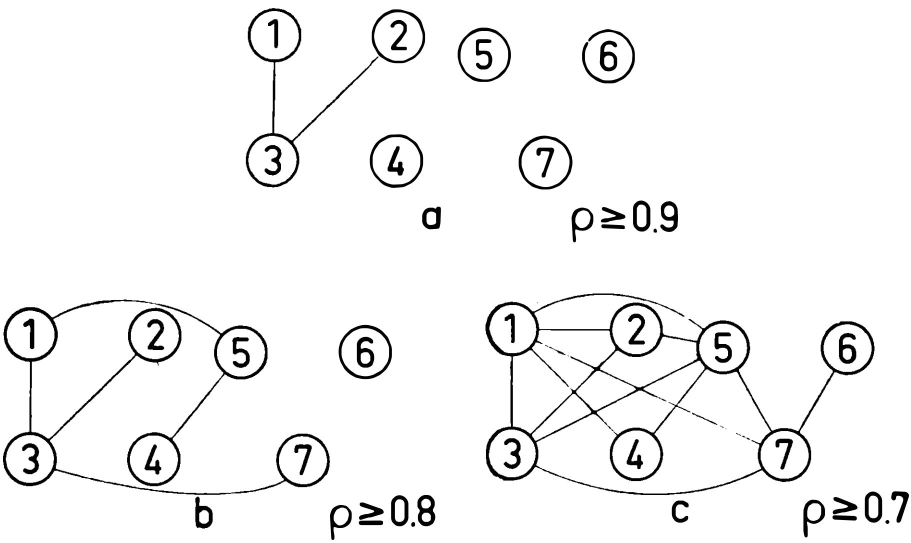

Fig. 6. Levels of correlation for the seven variates; *a*, $\varrho \geq 0.9$; *b*, $\varrho \geq 0.8$; *c*, $\varrho \geq 0.7$.

The sample mean vector

$$\bar{\mathbf{x}} = \begin{bmatrix} 3.479 \\ 0.613 \\ 0.588 \\ 0.282 \end{bmatrix}.$$

The sample covariance matrix

$$16\,\mathbf{S} = \begin{bmatrix} 4.1814 & 0.5071 & 0.8769 & 0.5502 \\ & 0.2824 & 0.2536 & 0.0978 \\ & & 0.2470 & 0.0535 \\ & & & 0.1981 \end{bmatrix}.$$

The sample correlation matrix

$$\mathbf{R} = \left[\begin{array}{cccc:ccc} 1.000 & 0.467 & 0.863 & 0.550 & 0.722 & 0.038 & 0.552 \\ & 1.000 & 0.960 & 0.414 & 0.497 & 0.414 & 0.222 \\ & & 1.000 & 0.242 & 0.559 & 0.430 & 0.650 \\ & & & 1.000 & 0.596 & 0.430 & 0.346 \\ \hdashline & & & & 1.000 & 0.393 & 0.528 \\ & & & & & 1.000 & 0.486 \\ & & & & & & 1.000 \end{array}\right].$$

The pattern of integration between variables is shown in Figs. 6, a—c (cf. p. 161).

The histograms all show relatively flat-topped forms, with x_3 deviating most strongly from the shape of the normal distribution. We note that x_1 is roughly normally distributed with a modal value at 3.68 cm. Clearly defined modal values do not occur for the distributions of the variables x_2, x_3, and x_4.

It is interesting to observe that the coefficient of variation for variable x_4 of this sample, and that for the other Santonian sample (sample 5), are the lowest of the entire study material.

Sample 4

LOCALITY. — Boguchar, 935-1b.

AGE. — Lower Campanian: Cmp_1.

NUMBER OF SPECIMENS. — 50.

Dimension	$\bar{x}$	s	V	Observed range
x_1	2.924 (2.786—3.062)	0.4793 (0.400—0.597)	16.39 ± 1.63	2.10—4.27
x_2	0.532 (0.512—0.552)	0.0686 (0.057—0.085)	12.89 ± 1.29	0.37—0.70
x_3	0.510 (0.481—0.529)	0.0656 (0.055—0.081)	12.86 ± 1.29	0.37—0.66
x_4	0.204 (0.175—0.233)	0.1015 (0.086—0.127)	49.75 ± 4.98	0.00—0.45
x_5	1.076 (0.982—1.170)	0.3219 (0.270—0.402)	29.92 ± 2.99	0.57—2.21
x_6	0.611 (0.548—0.674)	0.2200 (0.184—0.276)	36.01 ± 3.60	0.30—1.03
x_7	0.405 (0.366—0.444)	0.1353 (0.113—0.169)	33.41 ± 3.34	0.18—0.80

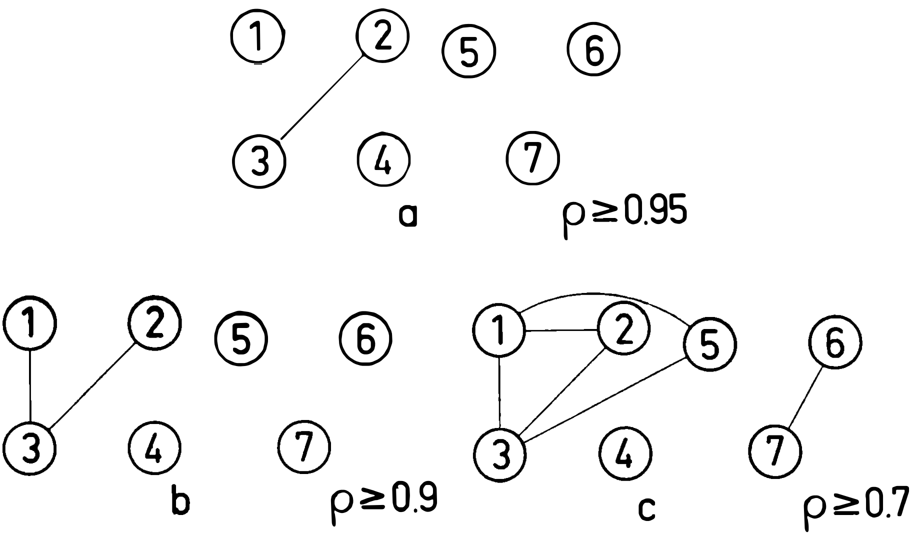

Fig. 7. Levels of correlation for the seven variates; *a*, $\varrho \geq 0.95$; *b*, $\varrho \geq 0.9$; *c*, $\varrho \geq 0.7$.

The sample mean vector

$$\bar{\mathbf{x}} = \begin{bmatrix} 2.924 \\ 0.532 \\ 0.510 \\ 0.204 \end{bmatrix}.$$

The sample covariance matrix

$$49\,\mathbf{S} = \begin{bmatrix} 11.1654 & 1.3135 & 1.3267 & 0.7507 \\ & 0.2297 & 0.2121 & 0.1101 \\ & & 0.2114 & 0.1081 \\ & & & 0.5050 \end{bmatrix}.$$

The sample correlation matrix

$$\mathbf{R} = \left[\begin{array}{cccc:ccc} 1.000 & 0.820 & 0.864 & 0.316 & 0.682 & 0.289 & 0.407 \\ & 1.000 & 0.962 & 0.323 & 0.343 & 0.227 & 0.346 \\ & & 1.000 & 0.331 & 0.641 & 0.189 & 0.291 \\ & & & 1.000 & 0.119 & 0.478 & 0.073 \\ \hdashline & & & & 1.000 & 0.149 & 0.288 \\ & & & & & 1.000 & 0.648 \\ & & & & & & 1.000 \end{array}\right].$$

The pattern of integration between variables is shown in Figs. 7, a—c (cf. p. 161).

The distribution of x_1 is a fairly good approximation to the normal curve, but those of x_2 and x_3 are very flat-topped. That the latter is so is a little surprising as the distributions of x_5 and x_6 are good approximations to the normal distribution. The distribution of x_4 is very drawn out laterally, which is a reflection of the wide range of values for this variable in sample 4. There seems, however, to be a fairly well defined modal value at about 0.22 cm, which lies exactly at the midpoint of the distribution.

Remaining modes are, x_1 (2.75 cm), x_2 (0.55 cm); hence, the distribution of variable x_1 skews slightly to the left (mean $=$ 2.92 cm) and that of variable x_2 skews slightly to the right (mean $=$ 0.53 cm). The other distributions do not show clearly defined modes.

Sample 5

Locality. — Lgov, N146/2.

Age. Santonian: Snt.

Number of specimens. — 23.

Dimensions	$\bar{x}$	s	V	Observed range
x_1	3.457 (3.302—3.612)	0.3504 (0.271—0.496)	10.14 ± 1.50	2.71—4.35
x_2	0.589 (0.551—0.627)	0.0866 (0.067—0.122)	14.70 ± 2.17	0.36—0.71
x_3	0.581 (0.546—0.616)	0.0800 (0.062—0.113)	13.77 ± 2.03	0.40—0.69
x_4	0.353 (0.296—0.414)	0.1327 (0.102—0.188)	37.59 ± 5.54	0.12—0.66
x_5	1.427 (1.277—1.577)	0.3401 (0.263—0.481)	23.83 ± 3.51	1.00—2.31
x_6	0.826 (0.754—0.898)	0.1634 (0.126—0.231)	19.78 ± 2.92	0.49—1.19
x_7	0.473 (0.411—0.535)	0.1407 (0.109—0.199)	29.75 ± 4.39	0.28—0.67

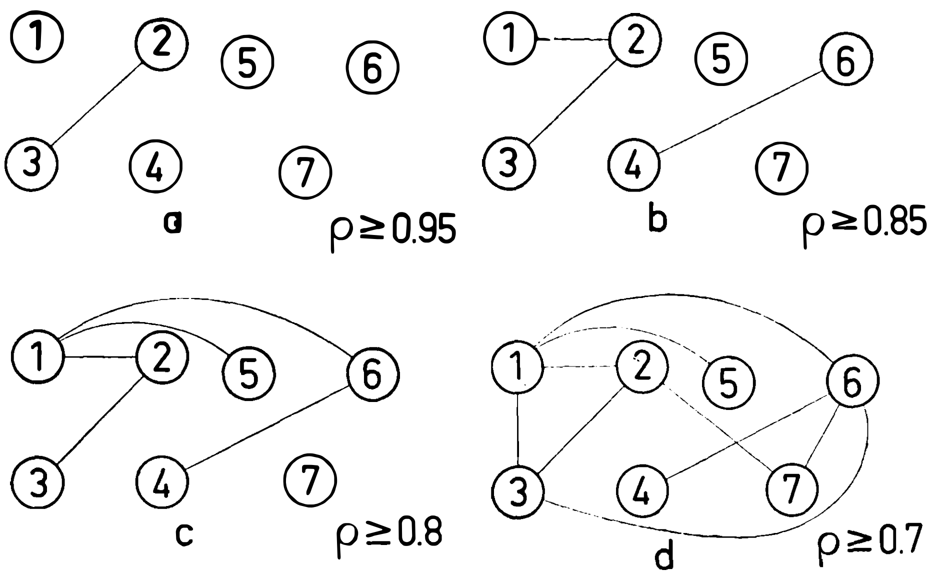

Fig. 8. Levels of correlation for the seven variates; *a*, $\varrho \geq 0.95$; *b*, $\varrho \geq 0.85$; *c*, $\varrho \geq 0.8$; *d*, $\varrho \geq 0.7$.

The sample mean vector

$$\bar{\mathbf{x}} = \begin{bmatrix} 3.457 \\ 0.589 \\ 0.581 \\ 0.353 \end{bmatrix}.$$

The sample covariance matrix

$$22\,\mathbf{S} = \begin{bmatrix} 2.7021 & 0.5141 & 0.4950 & 0.4580 \\ & 0.1652 & 0.1417 & 0.0520 \\ & & 0.1404 & 0.0447 \\ & & & 0.3875 \end{bmatrix}.$$

The sample correlation matrix

$$\mathbf{R} = \left[\begin{array}{cccc:ccc} 1.000 & 0.769 & 0.496 & 0.448 & 0.645 & 0.664 & 0.401 \\ & 1.000 & 0.932 & 0.206 & 0.207 & 0.512 & 0.403 \\ & & 1.000 & 0.192 & 0.382 & 0.512 & 0.359 \\ & & & 1.000 & 0.307 & 0.704 & 0.125 \\ \hdashline & & & & 1.000 & 0.293 & 0.050 \\ & & & & & 1.000 & 0.510 \\ & & & & & & 1.000 \end{array}\right].$$

The pattern of integration between variables is shown in Figs. 8, a—d (cf. p. 161).

The distribution of x_1 seems to be a fair approximation to the normal, as also that of x_3, while x_2 and more so, x_4, are poor approximations.

The mode and the mean coincide almost for the histogram of x_1 and lie at about 3.5 cm (mode = 3.54 cm, mean = 3.46 cm). The histogram for variable x_3 indicates a skewed distribution with the mode displaced to the right. The values for variable x_4 range widely and there is no clear modal value.

The mode for variable x_2 lies at 0.60 cm and that for the distribution of variable x_3 lies at 0.70 cm (mean = 0.58 cm).

SAMPLE 6

LOCALITY. — Don River (Kazanskaia), 922-1b.

AGE. — Lower Campanian: Cmp_1.

NUMBER OF SPECIMENS. — 24.

Dimension	$\bar{x}$	s	V	Observed range
x_1	2.908 (2.744—3.072)	0.3879 (0.308—0.556)	13.34 ± 1.92	2.40—4.02
x_2	0.520 (0.491—0.549)	0.0678 (0.053—0.095)	13.04 ± 1.88	0.40—0.65
x_3	0.503 (0.475—0.531)	0.0671 (0.052—0.094)	13.34 ± 1.92	0.40—0.64
x_4	0.198 (0.161—0.235)	0.0883 (0.069—0.125)	44.60 ± 6.44	0.08—0.39
x_5	1.080 (0.968—1.192)	0.2651 (0.206—0.372)	24.55 ± 3.54	0.84—1.59
x_6	0.595 (0.545—0.645)	0.1175 (0.091—0.165)	19.75 ± 2.95	0.43—0.88
x_7	0.402 (0.353—0.451)	0.1063 (0.082—0.149)	26.44 ± 3.95	0.23—0.66

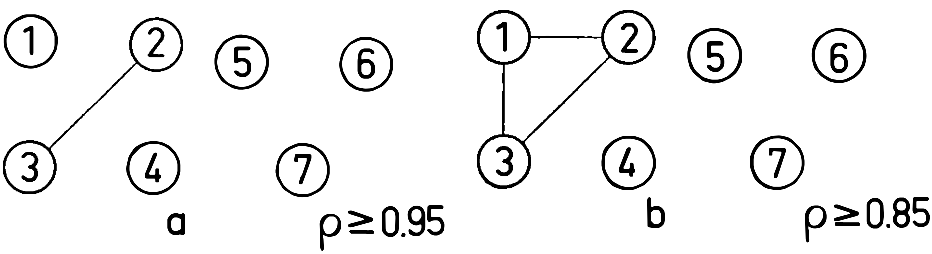

Fig. 9. Levels of correlation; *a*, $\varrho \geq 0.95$; *b*, $\varrho \geq 0.85$.

The sample mean vector

$$\bar{\mathbf{x}} = \begin{bmatrix} 2.908 \\ 0.520 \\ 0.503 \\ 0.198 \end{bmatrix}.$$

The sample covariance matrix

$$23\,\mathbf{S} = \begin{bmatrix} 3.6116 & 0.4929 & 0.5032 & 0.3900 \\ & 0.1061 & 0.1008 & 0.0461 \\ & & 0.1030 & 0.0584 \\ & & & 0.1838 \end{bmatrix}.$$

The sample correlation matrix

$$\mathbf{R} = \begin{bmatrix} 1.000 & 0.796 & 0.804 & 0.479 \\ & 1.000 & 0.965 & 0.330 \\ & & 1.000 & 0.424 \\ & & & 1.000 \end{bmatrix}.$$

It will observed that this correlation matrix concerns only the variables $x_1, \cdot \cdot, x_4$.

The pattern of integration between variables is shown in Figs. 9, a—b (cf. p. 161).

The histograms suggest that the distributions of all four variables correspond fairly well to that of the normal distribution. The histogram of variable x_1 indicates a certain amount of skewing to the left, although a well defined modal value occurs at 2.85 cm (mean $=$ 2.91 cm), near to the center of the distribution. The distribution of variable x_4 is also slightly skewed to the left; it differs from most of the sets of variable x_4 in ranging much less widely.

The remaining modal values are, x_2 (0.47 cm), x_3 (0.47 cm), while variable x_4 does not give a clearly defined mode.

SAMPLE 7

LOCALITY. — River Sura, 8012.

AGE. — Upper Coniacian: Cn_2.

NUMBER OF SPECIMENS. — 28.

Dimension	$\overline{x}$	s	V	Observed range
x_1	2.985 (2.738—3.232)	0.6261 (0.495—0.852)	20.60 ± 2.75	2.16—4.58
x_2	0.508 (0.459—0.557)	0.1233 (0.097—0.168)	24.27 ± 3.24	0.29—0.79
x_3	0.499 (0.346—0.652)	0.3869 (0.306—0.526)	77.53 ± 10.36	0.28—0.77
x_4	0.236 (0.182—0.290)	0.1378 (0.109—0.187)	58.38 ± 7.80	0.00—0.69
x_5	1.188 (1.067—1.309	0.3072 (0.243—0.418)	25.86 ± 3.46	0.69—2.05
x_6	0.646 (0.577—0.715)	0.1752 (0.139—0.238)	27.12 ± 3.63	0.33—1.18
x_7	0.406 (0.351—0.461)	0.1404 (0.110—0.191)	34.58 ± 4.62	0.18—0.85

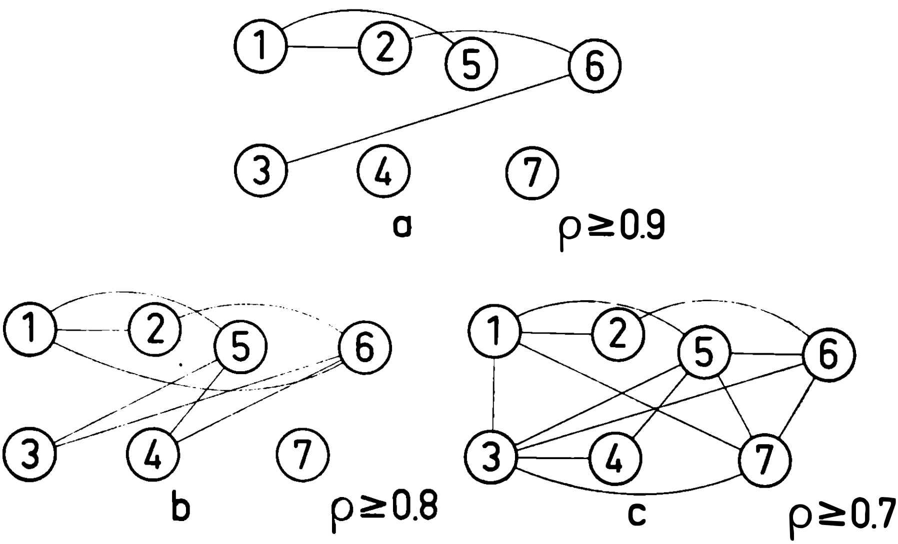

Fig. 10. Levels of correlation for the seven variates; *a*, $\varrho \geq 0.9$; *b*, $\varrho \geq 0.8$; *c*, $\varrho \geq 0.7$.

The sample mean vector is

$$\bar{\mathbf{x}} = \begin{bmatrix} 2.985 \\ 0.508 \\ 0.499 \\ 0.236 \end{bmatrix}.$$

The sample covariance matrix

$$27\,\mathbf{S} = \begin{bmatrix} 10.5863 & 1.8354 & 1.2271 & 0.4899 \\ & 0.4101 & 0.4592 & 0.1401 \\ & & 4.0410 & 0.2104 \\ & & & 0.5123 \end{bmatrix}.$$

The sample correlation matrix

$$\mathbf{R} = \left[\begin{array}{cccc:ccc} 1.000 & 0.881 & 0.593 & 0.390 & 0.874 & 0.730 & 0.463 \\ & 1.000 & 0.357 & 0.294 & 0.395 & 0.817 & 0.426 \\ & & 1.000 & 0.459 & 0.754 & 0.807 & 0.470 \\ & & & 1.000 & 0.773 & 0.678 & -0.201 \\ \hdashline & & & & 1.000 & 0.474 & 0.572 \\ & & & & & 1.000 & 0.565 \\ & & & & & & 1.000 \end{array}\right].$$

The pattern of morphological integration between variables is shown in Figs. 10, a—c (cf. p. 161).

All distributions seem to be moderately good approximations to the normal distribution, but with a tendency to flat-toppedness. The histogram for variable x_4 is interesting in that it represents the best approximation to the normal distribution of any of the samples of that variate. Variable x_3 shows a slight tendency towards skewing to the left.

The mode for x_1 lies at 2.7 cm, that for variable x_2 at 0.50 cm, that for variable x_3 at 0.55 cm, and that of x_4 at 0.18 cm. 27 of the observations for variable x_4 lie within the range of 0.00—0.40 cm, but one specimen measures 0.69 cm.

Sample 8

Locality. — Don River, 917b.

Age. — Lower Campanian: Cmp_1.

Number of specimens. — 11.

Dimension	$\bar{x}$	s	V	Observed range
x_1	2.918	0.4418	15.14	2.12—3.52
	(2.607—3.229)	(0.324—0.813)	± 3.39	
x_2	0.528	0.0938	17.77	0.39—0.69
	(0.462—0.594)	(0.069—0.173)	± 3.98	
x_3	0.485	0.0742	15.30	0.37—0.59
	(0.433—0.537)	(0.054—0.136)	± 3.42	
x_4	0.158	0.0721	45.63	0.05—0.30
	(0.107—0.209)	(0.053—0.133)	± 10.21	
x_5	1.065	0.1490	25.95	0.66—1.63
	(0.874—1.256)	(0.189—0.476)	± 5.70	
x_6	0.574	0.1490	25.95	0.34—0.86
	(0.469—0.679)	(0.104—0.261)	± 5.81	
x_7	0.414	0.1625	39.25	0.14—0.74
	(0.299—0.529)	(0.114—0.285)	± 8.78	

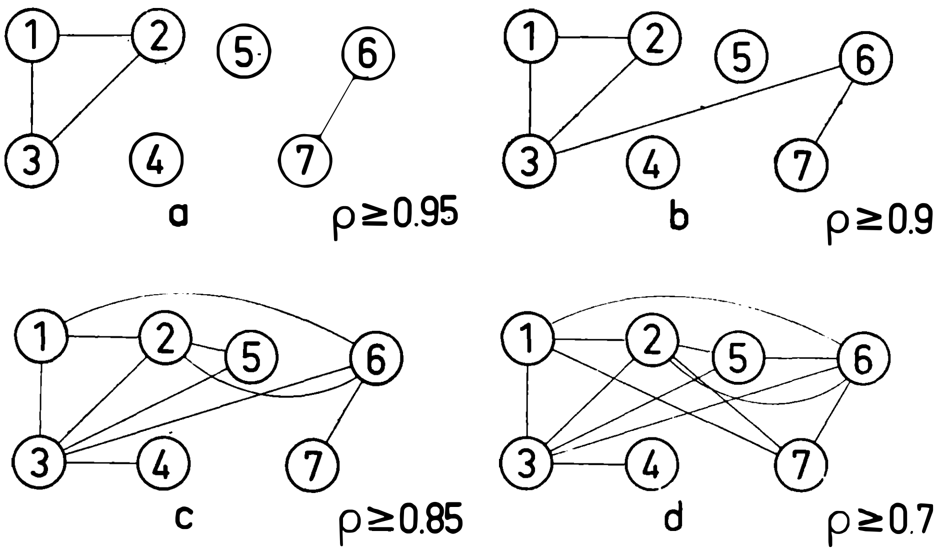

Fig. 11. Levels of correlation for the seven variates; *a*, $\varrho \geq 0.95$; *b*, $\varrho \geq 0.9$; *c*, $\varrho \geq 0.85$; *d*, $\varrho \geq 0.7$.

The sample mean vector

$$\bar{\mathbf{x}} = \begin{bmatrix} 2.918 \\ 0.528 \\ 0.485 \\ 0.158 \end{bmatrix}.$$

The sample covariance matrix

$$10\,\mathbf{S} = \begin{bmatrix} 2.1472 & 0.4138 & 0.3136 & 0.1049 \\ & 0.0968 & 0.0706 & 0.0102 \\ & & 0.0601 & 0.0174 \\ & & & 0.0574 \end{bmatrix}.$$

The sample correlation matrix

$$\mathbf{R} = \left[\begin{array}{cccc:ccc} 1.000 & 0.908 & 0.873 & 0.205 & 0.063 & 0.599 & 0.405 \\ & 1.000 & 0.925 & 0.137 & 0.712 & 0.605 & 0.485 \\ & & 1.000 & 0.587 & 0.625 & 0.768 & 0.237 \\ & & & 1.000 & 0.230 & 0.168 & -0.435 \\ \hdashline & & & & 1.000 & 0.515 & 0.368 \\ & & & & & 1.000 & 0.897 \\ & & & & & & 1.000 \end{array}\right].$$

The pattern of morphological integration between variables is shown in Figs. 11, a—d (cf. p. 161).

Summarizing remarks

The histograms indicate that the approximations to the normal distribution are generally fair to good, but occasionally poor. The deviations may be a reflection of sorting with respect to different characters. This subject will be taken up further on in several connexions. The overall very high coefficients of variation for x_4 are partly due to the smallness of this dimension and also to its mostly considerable variability.

The fact that the coefficients of variation do not vary regularly from sample to sample may also be a reflection of the effects of sorting. The diagrams based on the correlation coefficients indicate that x_2 and x_3 seem to be highly correlated; this is apparent in seven of the samples while sample seven would seem to be anomalous in this respect. Almost equally as strong correlation is displayed between x_1 and x_2 and x_1 and x_3, although the correlations between the respective pairs of variables are more variable from sample to sample. Intergroup correlation at the highest level of correlation studied occurs only in the anomalous sample seven. In the other seven samples intergroup correlation does not become apparent until a relatively low level of correlation has been attained.

The correlations between any pair of variables from sample to sample may be arranged in runs (cf. FELLER, 1959; OLSON and MILLER, 1958), whereby, the only states interesting us are those of "significantly correlated" ($= C$) and "uncorrelated" ($= O$), as ascertained from DAVID's (1937) tables of the correlation coefficient. The complete set of correlation coefficients for any sample may also be ordered in runs and then compared with the sequences from other samples. The correlation runs within samples are shown in the following table.

Table of correlation runs

Sample no.	Age	Runs ($r_{12}r_{13}r_{14}r_{23}r_{24}r_{34}$)
1	Campanian	CCCOOC
2	Campanian	COOCOO
4	Campanian	CCOCOO
6	Campanian	CCOCOO
8	Campanian	CCOCOC
3	Santonian	CCCCOO
5	Santonian	CCOCOO
7	Upper Coniacian	CCCOOC

It will be seen on perusal of the foregoing table that three samples have the identical run CCOCOO, two of them of Lower Campanian age and one deriving from a Santonian sample.

In the following table the runs formed by each correlation coefficient from sample to sample are shown.

Table of correlation runs

Correlation coefficient	Run (12468357)
r_{12}	CCCCCCCC
r_{13}	COCCCCCC
r_{14}	CCOOOCOC
r_{23}	OCCCCCCO
r_{24}	OOOOOOOO
r_{34}	COOOCOOC

Although the observations available are too few to permit quantitative testing several tentative conclusions may be drawn from the table above. The correlation coefficient r_{12} is significantly correlated in all samples and r_{13}, with its run COCCCCCC is also to be taken as significantly correlated. The sequence for r_{23} is also probably non-random. A non-random uncorrelated sequence would seem to be that for r_{24}, namely, OOOOOOOO. The correlation coefficient r_{14} forms 5 runs, as does also r_{34}; these two sequences would seem to be random.

Some univariate comparisons were made between samples. A comparison between large Campanian specimens (sample 1) and small Santonian specimens (sample 5) gave $t = 3.16$, which is significant. This therefore indicates that the lengths of rostra of the largest and the smallest occurrences differ. A comparison between rostral lengths of samples 3 and 5, both of Santonian age, gave $t = 0.46$, which is not significant. A t-test between Upper Coniacian and Santonian material was made (samples 7 and 3), a value of $t = 2.73$ being obtained for 44 degrees of freedom, which is probably significant. A univariate, single-classification analysis of variance was made on x_4 in samples 1—6, with 189 degrees of freedom. The analysis gave $F = 58.29$, which is highly significant, and which indicates that the degree of asymmetry of the alveolar scar varies strongly from sample to sample. This observation is taxonomically significant in connexion with the delineation of the various subspecies of *Actinocamax verus.*

In the following table the observed ranges for correlation coefficients are shown for the eight samples.

Correlation coefficient	observed range	correlation coefficient	observed range
r_{12}	0.467—0.933	r_{27}	0.074—0.485
r_{13}	0.296—0.873	r_{37}	0.111—0.625
r_{14}	0.205—0.550	r_{35}	—0.070—0.768
r_{15}	0.063—0.874	r_{36}	0.001—0.807
r_{16}	0.038—0.730	r_{37}	—0.583—0.650
r_{17}	0.108—0.552	r_{45}	—0.175—0.773
r_{23}	0.357—0.960	r_{46}	—0.435—0.704
r_{24}	—0.082—0.414	r_{47}	—0.453—0.515
r_{25}	—0.154—0.712	r_{57}	0.293—0.515
r_{26}	0.036—0.817	r_{67}	0.403—0.897

Very little material was available from sample 9, the Lower Coniacian locality on the Volga River. The averages of the four dimensions x_1, x_2, x_3, x_4 are shown in the following table. The sample size is 4.

$\bar{x}_1$	$\bar{x}_2$	$\bar{x}_3$	$\bar{x}_4$
4.025	0.658	0.665	0.200

It is instructive to plot the means of the samples against time in order to ascertain whether chronoclines in some or any of the dimensions exist. This is done in Fig. 12.

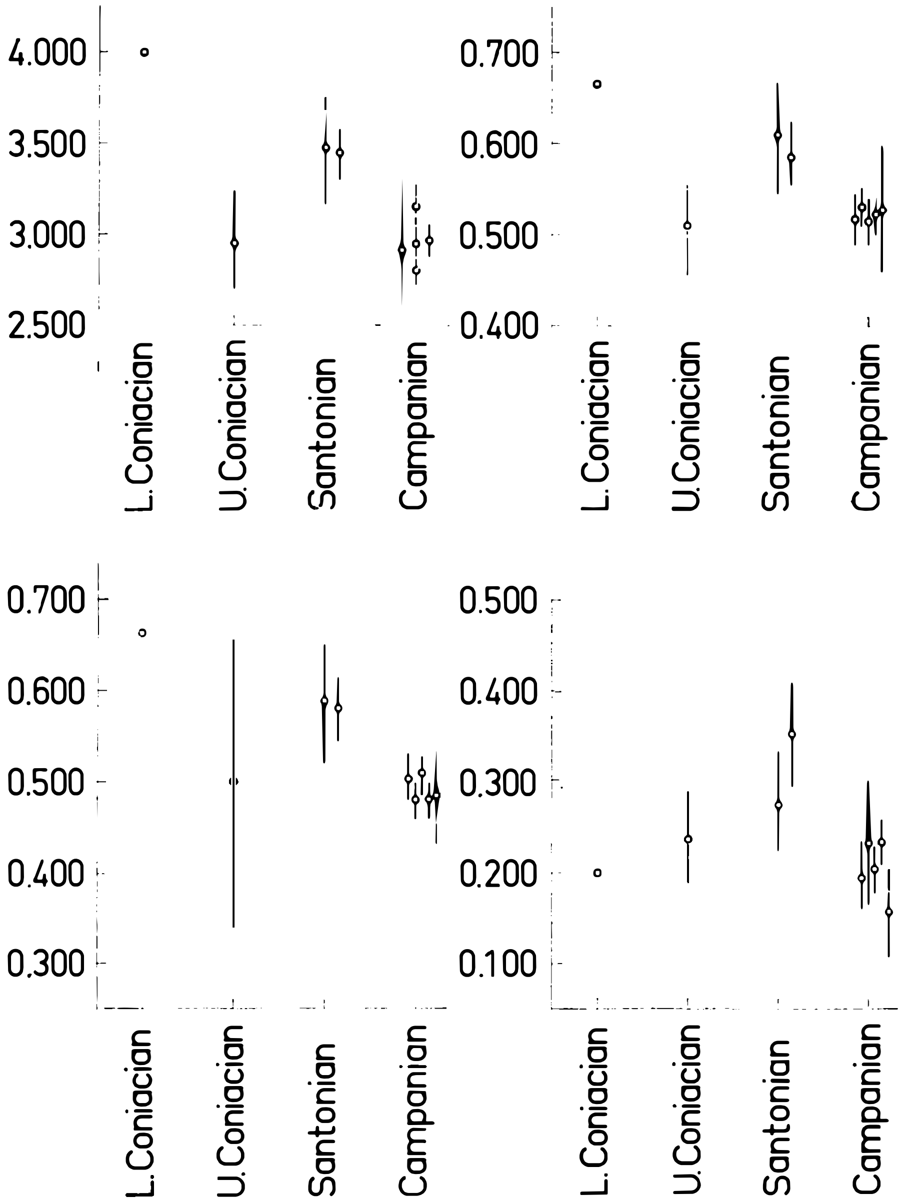

Fig. 12. Changes in the mean values of the dimensions x_1, x_2, x_3, and x_4 from Lower Coniacian to Lower Campanian time.

In all cases but that of the small Lower Coniacian sample ($N = 4$) the confidence boundaries are indicated in Fig. 12. Apart from the Upper Coniacian sample, there is a gradual general decrease in size for the variates x_1, x_2, and x_3, while the behavior of x_4 is more of an oscillatory nature. The reason for the difference in behavior in the first three variables and x_4 is probably to be sought in their different morphologic nature. The first three, x_1, x_2, and x_3, are typical size dimensions and an increase or decrease in them will tend to be followed mutually. As indicated by the morphologic-integrational work in the foregoing, and the principal component analysis in a succeeding chapter, x_4 is not strongly connected with the size dimensions and therefore cannot be expected to link up closely with their fluctuations. In Fig. 13 ,fluctuations in the quadrivariate mean vector are shown. The values of the mean vector are given in the table below.

Tables of lengths of quadrivariate mean vectors (x_1, x_2, x_3, x_4)

Lower Coniacian	Upper Coniacian	Santonian	Lower Campanian
4.137	3.078	3.592, 3.572	3.246, 2.897, 3.009, 2.924, 3.003

Fig. 13 also indicates the same approximate trend towards smaller size, from Lower Coniacian to Lower Campanian. Summing up, it would appear that a definite size trend exists from Lower Coniacian to Lower Campanian in which the dimensions of the rostrum gradually decrease; that is a negative size chronocline occurs.

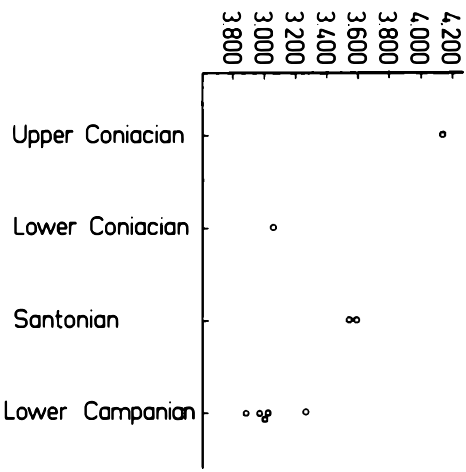

Fig. 13. Chronologic changes in the length of the mean vector for 9 samples from Lower Coniacian to Lower Campanian.

HOMOGENEITY OF COVARIANCE MATRICES

At an early stage in the study it became apparent that heterogeneity of covariance matrices could be expected. Therefore, the covariance matrices of the first 8 samples were investigated with the aid of the multivariate analog of the BARTLETT test for homogeneity. (For details, reference is made to ANDERSON (1958).) The highly significant value of $-2 \log_e W = 683.7$ was obtained ($\chi^2_{.975,70} = 90$). Examination of the covariance matrices indicates that the heterogeneity would seem mainly to arise from samples 7 and 8. These were excluded from the material and the calculations carried out again. This time $-2 \log_e W$ was found to be 82.22, which is indicative of a lesser degree of heterogeneity ($\chi^2_{.975,50} = 70$). Summing up, we have that samples 7 and 8 cause extensive heterogeneity in the pooled material. These were therefore excluded from the multivariate computations.

The three variables x_5, x_6, and x_7 were excluded from most of the multivariate calculations for the following reasons. The latter two were taken in order to supply a measure of the asymmetry of the alveolar scar, x_4, and it was therefore considered worthwhile economizing in the number of variables by excluding these two. The variable x_5 was excluded owing to the heterogeneity in the correlation coefficients formed by it with the other variables. Testing r_{15} for homogeneity in six samples gave $\chi^2 = 23.62$ ($k = 5$), which is highly significant.

In the present connexion the multivariate coefficients of scatter and the corresponding multivariate coefficients of variation were computed. They are:

Table of multivariate coefficients of variation and scatter

Sample	1	2	3	4	5	6	7	8
$V_4 \times 10^{-2}$	2.31	1.39	3.79	2.40	2.75	2.22	6.57	1.33
$\lvert\mathbf{R}\rvert^{\frac{1}{2}}$	0.38	0.27	0.41	0.13	0.18	0.13	0.39	0.03

The two extreme samples, 7 and 8, are shown by the above table to occupy the upper and lower extreme positions. The relatively low values of the coefficient of scatter are a reflection of the fairly high correlation between variables. This is one of the contributing causes to the low values of V_4, compared with the univariate coefficients of variation. Another contributory cause is that the values obtained of the multivariate coefficient of variation are dependent on a vector length, which is in its turn dominated by the largest component in the mean vector, namely, that of $\bar{x}_1$. One of the deficiencies of the univariate coefficient of variation is that comparisons between dimensions of different magnitude are unrealistic. In the present connexion comparisons between the coefficients of variation of x_1 and x_4 exaggerate the variability of the latter, owing to its much lesser size, even taking into consideration the generally relatively greater variance of x_1. The multivariate coefficient of variation therefore tends to supply a more cohesive picture of the covariability of the four variables.

The significance of the intercorrelation between variables may be tested by calculating the statistic (cf. ANDERSON, 1958):

$$V = \frac{|\mathbf{R}|}{\Pi\, |\mathbf{R}_{ii}|}\ .$$

The criterion V thus reduces to

$$V = |\mathbf{R}|.$$

Taking the two largest samples we can use asymptotic theory in calculating the significance. For samples 2 ($N = 52$) and 4 ($N = 50$), $|\mathbf{R}^{(2)}| = 0.0729$, and $|\mathbf{R}^{(4)}| = 0.0169$. One calculates $-m\log V$, which is distributed approximately as χ^2 with $f = \frac{1}{2}(p^2 - \Sigma p_i^2)$ degrees of freedom and where

$$m = N - \frac{3}{2} - \frac{p^3 - \Sigma p_i^3}{3\,(p^2 - \Sigma p_i^2)}\ .$$

For sample 2, $-m\log V^{(2)} = 127.93$ and for sample 4, $-m\log V^{(4)} = 197.08$, both of which are highly significant. There can therefore be no doubt of the dependence between the four variates for 6 degrees of freedom.

For comparison, the correlation matrix for the variables x_5, x_6 and x_7 for sample 4 was taken. For this we have that $|\mathbf{R}| = 0.527$. The number of degrees of freedom is 3 and $-m\log V = 29.98$. The significance point for χ^2 with 3 degrees of freedom is 11.3 on the .01 level of significance and the value obtained is highly significant; it may therefore be inferred that the variables are not independent.

Homogeneity of certain bivariate covariance matrices

In connexion with the chapter on generalized distances it is required to study certain two-dimensional matrices, namely, the matrices formed by the variate pair $x_1 - x_2$ and the variate pair $x_2 - x_3$. It was considered probable that the state of homogeneity of the four-dimensional covariance matrices considered in the foregoing could well be different from that of the two-dimensional matrices. In order to test this supposition the respective sets of matrices were analyzed for homogeneity.

The eight matrices for the variates x_1 and x_2 were found to be heterogeneous ($\chi^2 = 662.34$). The origin of the heterogeneity was not pinpointed directly, although it seems as though the matrices of samples 2, 3, and 7 might be the divergent ones. As a byproduct of the computations a table of bivariate coefficients of variation and scatter was drawn up. It is reproduced here.

Table of two-dimensional (x_1, x_2) coefficients of variation and scatter

Sample	1	2	3	4	5	6	7	8
$V_2 \times 10^{-2}$	7.46	11.96	13.88	11.23	8.60	9.46	14.39	8.30
$\|\mathbf{R}\|^{\frac{1}{2}}$	0.83	0.36	0.88	0.57	0.64	0.78	0.47	0.42

For the eight matrices of the variates x_2 and x_3 a result of heterogeneity was obtained. Elimination of sample 7 from the computations reduced the "level of heterogeneity", to give a chi-square of 40.70 ($\chi^2_{18,.05} = 28.87$). As in the foregoing connexion the coefficients of scatter and variation were computed; it was found that the values for sample 7 deviate widely from the others. The table of values is given below.

Table of two-dimensional (x_2, x_3) coefficients of variation and scatter

Sample	1	2	3	4	5	6	7	8
$V_2 \times 10^{-2}$	11.67	15.95	15.75	12.47	13.04	10.50	97.40	18.56
$\|\mathbf{R}\|^{\frac{1}{2}}$	0.66	0.37	0.28	0.27	0.36	0.61	0.93	0.38

Finally, it is of interest to observe that the septivariate coefficient of variation for sample 4 ($N = 50$) is $V_7 = 21.24 \times 10^{-2}$, which is higher than in the quadrivariate case and indicates a lesser overall degree of correlation between variables.

Summarizing remarks

Owing to the existence of heterogeneity in the four-dimensional covariance matrices in the eight samples it was found necessary to analyse these in order to detect the diverging samples. This was attempted with the aid of the determinants of the covariance matrices; the investigation permitted localization of the divergencies to two samples. The heterogeneity is here considered to have arisen mainly from the effects of sorting but also as a result of evolutionary processes. But, although sorting of the belemnite rostra is indicated, the fact that they are mostly excellently preserved speaks against more than slight transport, without much attrition. Tests for independence of variables were made for x_1, x_2, x_3, and x_4 in two samples and one test for independence of variables in a large sample of x_5, x_6, and x_7. These tests indicate an overall relatively high degree of dependency between variables and support the results of the study on integration between variables.

Tests of homogeneity of covariance matrices for two bivariate sets of the variate pairs x_1, x_2 and x_2, x_3 indicate that in the former case the degree of heterogeneity is high. The heterogeneity could not be much reduced by excluding matrices 7 and 8, the diverging matrices of the four-dimensional investigation. For the latter pair eliminating sample 7 from the computations lowered the "degree of heterogeneity" considerably.

In the type of material studied in the present paper one may therefore suspect that changes in the number of variables may influence the conditions of homogeneity in the covariance matrices.

For further remarks on heterogeneous covariance matrices in paleontologic biometry reference is made to REYMENT (1962).

PRINCIPAL COMPONENT STUDY

The principal component analysis was carried out on the matrix of products and cross products for the sample Boguchar 935-1b. This differs only from the covariance matrix by being 49 times greater than it ($N = 50$). Also the septivariate correlation matrix for the sample Boguchar 931-1b, and 9 quadrivariate matrices of sums and products. The order of variables is x_1, x_5, x_2, x_3, x_6, x_4, x_7.

$$\mathbf{A} = \begin{bmatrix} 11.1654 & 5.1323 & 1.3135 & 1.3267 & 1.4875 & 0.7507 & 1.2875 \\ 5.1323 & 5.0764 & 0.5957 & 0.6639 & 0.5187 & 0.1913 & 0.6144 \\ 1.3135 & 0.5957 & 0.2297 & 0.2121 & 0.1677 & 0.1101 & 0.1570 \\ 1.3267 & 0.6639 & 0.2121 & 0.2114 & 0.1337 & 0.1081 & 0.1265 \\ 1.4875 & 0.5187 & 0.1677 & 0.1337 & 2.3740 & 0.5229 & 0.9443 \\ 0.7507 & 0.1913 & 0.1101 & 0.1081 & 0.5229 & 0.5050 & 0.0492 \\ 1.2875 & 0.6144 & 0.1570 & 0.1265 & 0.9443 & 0.0492 & 0.8956 \end{bmatrix}.$$

The principal components extracted from it are not identical with those obtainable from the covariance matrix but they are of the same relative magnitude. The eigenvalues of $\mathbf{A}$ are (N-1) times those of $\mathbf{S}$, respectively; the eigenvectors from each matrix are the same. The eigenvalues and eigenvectors were extracted by program Q 10 (JACOBI method) on the BESK and FACIT electronic computers.

Table of eigenvalues and eigenvectors for Boguchar 935-1b

Eigenvalue	Corresponding eigenvector						
14.8141	0.8482	0.4755	0.1005	0.1028	0.1346	0.0577	0.1109
2.7421	0.1087	—0.5081	0.0144	—0.0109	0.7756	0.1813	0.3087
1.9925	—0.4851	0.7140	—0.0650	—0.0540	0.4533	0.0044	0.2055
0.5906	0.0298	—0.0726	—0.0184	—0.0500	—0.1790	—0.6713	0.7130
0.2029	—0.1145	0.0142	0.2065	0.1536	—0.3627	0.6800	0.5714
0.1095	—0.1386	—0.0129	0.7400	0.5972	0.1060	—0.2252	—0.1202
0.0058	0.0300	—0.0726	—0.0184	—0.0500	—0.1790	—0.6713	0.7130

Before proceeding with the interpretation of the results of the matrix operations a few words concerning the concepts involved in principal component analysis might be in place. The method was originally introduced as an alternative to the mathematically related procedure of Factor Analysis, in the treatment of psychometric data. Both procedures are, as first proposed, "semi-statistical" techniques in that they do not take stochastic variation into account. Factor analysis was first applied to biologic data some 25 years ago. Only the largest eigenvalue (and eigenvector) was extracted from the correlation matrix of the studied variables, the elements of this correlation always being positive (the "general factor" of psychometric analysis). Later applications of factor analysis have also been made to include subsequent eigenvalues and their corresponding eigenvectors.

The application of principal component analysis to biologic materials is basically the same as for factor analysis. Here one uses either the covariance matrix or the correlation matrix of the variables involved; in the latter case the components of the eigenvectors should be adjusted by dividing each element by the pertinent standard deviation. Although there is no concrete reason for the assumption, this "component" is attributed to size variation, hence variation traceable to environmental causes. The subsequent eigenvectors have positive and negative elements and are usually interpreted as being shape components, representative of "internal" variability. This explanation of the mathematical results is not without arbitrariness, for shape variation can in some organisms be caused by environmetal stimuli.

The results of the shape and size analysis of the data are presented in the following table.

Tabular summary of size and shape variation in *Actinocamax verus laevigatus* ARKHANGELSKI

Principal axes of ellipsoid	first	second	third	fourth	fifth	sixth	seventh
Magnitude of variance	14.8141	2.7421	1.9925	0.5906	0.2029	0.1095	0.0058
Percentage of total variance	72.414	13.404	9.740	2.887	0.992	0.535	0.028
Nature of the variation	simultaneous size variation of all dimensions	mainly shape variation in site of maximum inflation and alveolar scar	mainly shape variation in rostral length, site of maximum inflation and alveolar scar	mainly shape variation in asymmetry of alveolar scar	mainly size fluctuation in alveolar scar	mainly joint size variation in breadth and width of rostrum	mainly shape variation in breadth and width of rostrum
Approximate lengths of axes of ellipsoid	5.6014	2.4100	2.0542	1.1184	0.6556	0.4816	0.1108

Regarding the equations of the axes of the ellipsoid,

$$\frac{x_1 - \bar{x}_1}{b_{11}} = \cdot \quad \cdot \cdot \cdot \cdot = \frac{x_7 - \bar{x}_7}{b_{17}} = y_1 - \bar{y}_1 ,$$

where the b_{ij} refer to the appropriate elements of the pertinent eigenvector, the variation may be analysed in the ensuing terms. The equation of the major axis of the ellipsoid represents a simultaneous increase in all variables, most of the variation occurring in the two measures of rostral length, length of rostrum and site of maximum inflation of the rostrum, whereas the other five dimensions make contributions of about the same magnitude. This principal component is interpreted as a growth trend.

The second axis represents mainly variation in site of maximum inflation and one of the alveolar measurements, namely, that representing the lower edge of the alveolar scar. In a sense it is a shape component whereby a decrease in the distance of the site of maximum inflation from the alveolar scar tip is simultaneously followed by an increase in the length of the long side of the alveolar scar. This variation is positively followed to a lesser extent by the other side of the alveolar scar; the contributions of the other variables are not important. These two principal components account for almost 86 percent of the total variation.

The third principal component represents mostly variation in rostral length, site of maximum inflation and the long margin of the alveolar scar, with a lesser contribution from the short margin of the scar; the contributions of the remaining variables are almost zero. In this connexion joint positive variation in the latter three variables is simultaneously accompanied by negative variation in rostral length, and vice versa. This is also a shape component. The first three principal components cover almost 96 % of the total variation.

For the fourth axis the variation is principally concentrated to the asymmetry of the alveolar scar and the length of the shorter scar margin, with a less important contribution from the opposite margin. This is a shape component, a negative change in the asymmetry of the scar being accompanied by a positive change of about the same magnitude in the shorter margin and a much smaller negative shift in the other margin. The other variables contribute little to this variation.

The variation represented by the fifth axis is roughly the same as for the fourth, but with the difference that we have simultaneous positive variation in the asymmetry variable and that of the shorter scar margin accompanied by negative variation in the other margin. The contributions of the other variables are larger than before, the main effect deriving from the two width dimensions.

The sixth axis represents mainly positive covariation between the two dimensions rostral width and rostral breadth. It is interesting that these two dimensions contribute so little to the total variation.

The final principal component is for the most part concerned with shape variation in the alveolar scar.

The transformed variables

In the present study an effective reduction in the number of variables from seven to three has been accomplished, as 96 % of the total variation is contained in the first three principal components. These three transformed variables are:

$$\begin{aligned} y_1 &= 0.848x_1+0.100x_2+0.103x_3+0.058x_4+0.476x_5+0.135x_6+0.111x_7,\\ y_2 &= 0.109x_1+0.014x_2-0.011x_3+0.181x_4-0.508x_5+0.776x_6+0.309x_7,\\ y_3 &= -0.485x_1-0.065x_2-0.054x_3+0.004x_4+0.714x_5+0.453x_6+0.205x_7. \end{aligned}$$

The transformed variables are uncorrelated.

The results of the principal component analysis also suggest that the dimensions studied may be roughly partitioned into two groups, the one concerned with the size dimensions of the rostrum and the other with the variation in the asymmetry of the alveolar scar.

Principal components of the correlation matrix

The principal components of the correlation matrix of sample Boguchar 931-1b were computed. The first eigenvalue, $\lambda_1 = 3.004046$, accounts for only 42.91 % of the total variation. The second eigenvalue $\lambda_2 = 2.030030$, accounts for 29.00 % of the total variation. The third eigenvalue $\lambda_3 = 1.201689$, accounts for 17.17 % of the total variation. The three first principal components thus represent 89.08 % of the entire variation, the remaining 10.02 % being attached to the last four components. This is certainly quite different from the results found using a covariance matrix. The first three transformed variables are

$$\begin{aligned} y_1 &= 0.520x_1+0.506x_2+0.388x_3+0.208x_4+0.403x_5+0.298x_6+0.171x_7,\\ y_2 &= 0.074x_1-0.252x_2-0.527x_3+0.056x_4+0.075x_5-0.470x_6+0.651x_7,\\ y_3 &= -0.164x_1-0.209x_2+0.026x_3+0.833x_4-0.079x_5+0.332x_6-0.344x_7. \end{aligned}$$

With respect to the first transformed variable it will be observed that the equation derived from the correlation matrix attributes greater importance to x_2 and somewhat less importance to x_1. The second and third variables differ even more extensively.

Quadrivariate principal component analysis

Eight quadrivariate covariance matrices were subjected to principal component analysis. It was found that the eigenvector patterns resulting could be ordered into two groups, the one comprising all Campanian samples plus one Santonian, and the other comprising a Santonian sample, an Upper Coniacian sample and a sample made up of the pooled (within) covariance matrices of the entire study material.

Group 1

Sample	eigenvalues	percentage of total variation	eigenvectors
(1) Campanian	$\lambda_1 = 0.073034$	76.74	$\mathbf{b}_1 = (\ 0.9320,\ 0.1048,\ 0.0908,\ 0.3348)$
	$\lambda_2 = 0.019525$	20.52	$\mathbf{b}_2 = (-0.3088, -0.1949, -0.0352,\ 0.9303)$
	$\lambda_3 = 0.002263$	2.39	$\mathbf{b}_3 = (-0.1894,\ 0.8074,\ 0.5441,\ 0.1269)$
	$\lambda_4 = 0.000356$	0.04	$\mathbf{b}_4 = (\ 0.0091, -0.5469,\ 0.8333, -0.0800)$
(4) Campanian	$\lambda_1 = 0.235389$	95.23	$\mathbf{b}_1 = (\ 0.9836,\ 0.1172,\ 0.1181,\ 0.0693)$
	$\lambda_2 = 0.009265$	3.75	$\mathbf{b}_2 = (-0.0814,\ 0.0521,\ 0.0433,\ 0.9944)$
	$\lambda_3 = 0.002368$	0.96	$\mathbf{b}_3 = (-0.1599,\ 0.7603,\ 0.6244, -0.0801)$
	$\lambda_4 = 0.000152$	0.06	$\mathbf{b}_4 = (-0.0166, -0.6367,\ 0.7709, -0.0015)$
(6) Campanian	$\lambda_1 = 0.165006$	94.77	$\mathbf{b}_1 = (\ 0.9750,\ 0.1354,\ 0.1383,\ 0.1093)$
	$\lambda_2 = 0.006122$	3.52	$\mathbf{b}_2 = (-0.0976, -0.0899, -0.0072,\ 0.9911)$
	$\lambda_3 = 0.002843$	1.63	$\mathbf{b}_3 = (-0.1997,\ 0.7204,\ 0.6623,\ 0.0505)$
	$\lambda_4 = 0.000137$	0.08	$\mathbf{b}_4 = (-0.0045, -0.6743,\ 0.7363, -0.0063)$
(8) Campanian	$\lambda_1 = 0.227928$	96.52	$\mathbf{b}_1 = (\ 0.9703,\ 0.1888,\ 0.1435,\ 0.0478)$
	$\lambda_2 = 0.005493$	2.33	$\mathbf{b}_2 = (\ 0.0047, -0.2579, -0.0142,\ 0.9660)$
	$\lambda_3 = 0.002330$	0.99	$\mathbf{b}_3 = (-0.2390,\ 0.6552,\ 0.6921,\ 0.1862)$
	$\lambda_4 = 0.000398$	0.16	$\mathbf{b}_4 = (\ 0.0371, -0.6845,\ 0.7073, -0.1726)$
(5) Santonian	$\lambda_1 = 0.135426$	87.75	$\mathbf{b}_1 = (\ 0.9504,\ 0.1858,\ 0.1777,\ 0.1747)$
	$\lambda_2 = 0.014514$	9.40	$\mathbf{b}_2 = (-0.1012, -0.1946, -0.1953,\ 0.9559)$
	$\lambda_3 = 0.003933$	2.55	$\mathbf{b}_3 = (-0.2926,\ 0.7317,\ 0.5693,\ 0.2343)$
	$\lambda_4 = 0.000454$	0.30	$\mathbf{b}_4 = (-0.0284, -0.6262,\ 0.7786,\ 0.0286)$

Group 2

Sample	eigenvalues	percentage of total variation	eigenvectors
(3) Santonian	$\lambda_1 = 0.282028$	90.98	$\mathbf{b}_1 = (\ 0.9611,\ 0.1306,\ 0.2070,\ 0.1281)$
	$\lambda_2 = 0.018494$	5.97	$\mathbf{b}_2 = (-0.2107,\ 0.8397,\ 0.4949, -0.0748)$
	$\lambda_3 = 0.009451$	3.05	$\mathbf{b}_3 = (-0.0914,\ 0.2321, -0.2932,\ 0.9229)$
	$\lambda_4 = 0.000005$	0.00	$\mathbf{b}_4 = (-0.1535, -0.4732,\ 0.7914,\ 0.3553)$
(7) Upper Coniacian	$\lambda_1 = 0.413629$	71.82	$\mathbf{b}_1 = (\ 0.9671,\ 0.1733,\ 0.1792,\ 0.0503)$
	$\lambda_2 = 0.141730$	24.61	$\mathbf{b}_2 = (-0.1892,\ 0.0316,\ 0.9808,\ 0.0356)$
	$\lambda_3 = 0.017990$	3.12	$\mathbf{b}_3 = (-0.0592,\ 0.0947, -0.0505,\ 0.9925)$
	$\lambda_4 = 0.002565$	0.45	$\mathbf{b}_4 = (-0.1592,\ 0.9798, -0.0585, -0.1060)$
Total pooled	$\lambda_1 = 0.183085$	84.75	$\mathbf{b}_1 = (\ 0.9694,\ 0.1666,\ 0.1518,\ 0.0974)$
	$\lambda_2 = 0.019636$	9.09	$\mathbf{b}_2 = (-0.1741,\ 0.1305,\ 0.9760, -0.0119)$
	$\lambda_3 = 0.011385$	5.26	$\mathbf{b}_3 = (-0.0845, -0.0974,\ 0.0100,\ 0.9916)$
	$\lambda_4 = 0.001934$	0.90	$\mathbf{b}_4 = (-0.1512,\ 0.9725, -0.1560,\ 0.0843)$

If we examine the principal components of the first group we find that the first principal component is one of size variation with most of the variation occurring in x_1 (0.9320—0.9836) the contributions of any of the other three variables being only a fifth of this, except for x_4 of sample (1). The second principal component is a shape factor with almost all variation being centered around x_4, with small contributions of opposite sign from x_1, x_2, x_3. The third principal component represents shape variation, positive large increases in x_2 and x_3 of about the same magnitude being accompanied by a small negative increase in x_1 and usually a small positive increase in x_4. The fourth principal component is also a shape factor which again is concerned with x_2 and x_3, but this time a positive increase in one is accompanied by a roughly equally large negative increase in the other. In all cases the absolute value of x_3 is slightly greater than that of x_2.

For the principal components of group 2 we have that the first principal component is mainly representative of variation in x_1, as is so for group 1. The second principal component differs in being mainly concerned with variation in x_3 and the third principal component differs in representing almost entirely variation in x_3. The fourth principal component is in two cases indicative of variation mainly in x_2 and in one case of variation in x_2 and x_3.

Summing up, it would seem that the geologically younger representatives of *A. verus* display one pattern of variation and the geologically older representatives another. The two Santonian samples are not exactly typical of either of the groups with which they have here been placed and may possibly be transitional. The fact that the principal components of the pooled sample have the pattern of those of the older representatives may possibly be suggestive of a tendency to subspeciation in *A. verus* in Upper Santonian-Lower Campanian time. Morphologic differentiation is obscured by pooling and the Upper Coniacian type of variation is simulated. These results support the subspecific delineation proposed in the descriptive section.

It is instructive to examine some of the angles between eigenvectors with reference to agreement and diversity in size and shape. In the following table the angles between the pooled sample's ($N = 221$) eigenvectors corresponding to λ_1, respectively, λ_2 and each of the samples are given.

			Between $\mathbf{b}_1^P$ and $\mathbf{b}_1^k$			
1	4	6	8	5	3	7
14°41′	3°52′	2°03′	2°44′	4°59′	4°12′	3°09′
			Between $\mathbf{b}_2^P$ and $\mathbf{b}_2^k$			
82°50′	87°02′	89°14′	86°34′	77°44′	50°56′	6°19′

The interesting point arising out of this is that the size vectors for all samples are more or less parallel, allowing for sampling and stochastic errors. However, the first shape vector shows a clear delineation into two groups, agreeing with the time groups already noted, in which one set of vectors lies nearly at right angles to the other set, with the Santonian samples tending to occupy an intermediate position. This implies that the younger group displays a different mode of shape variation from the older group.

Using the two first principal components of the pooled belemnite sample as a base,

$$z_1 = 0.97x_1 + 0.17x_2 + 0.15x_3 + 0.10x_4$$
$$z_2 = -0.17x_1 + 0.13x_2 + 0.98x_3 - 0.01x_4$$

$\bar{z}_1$ and $\bar{z}_2$ were computed for each sample and plotted as shown in fig. 14. There is an obvious clustering of the Santonian samples to the right and of the Campanian samples to the left, with sample 1 occupying a somewhat anomalous position. It is interesting that sample 7 of Coniacian age falls together with the Campanian group.

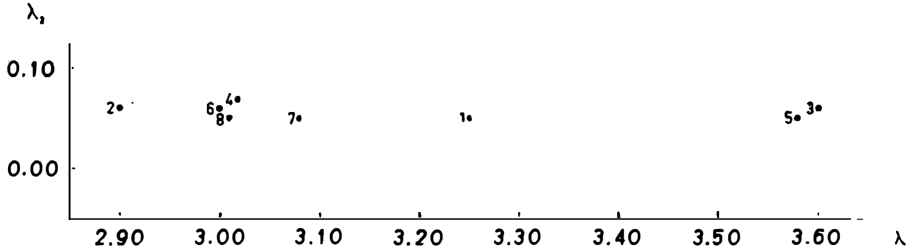

Fig. 14. "Group constellations" for belemnite occurrences with principal components as axes (pooled belemnite sample as base).

DIFFERENCES IN MEAN VECTORS

The mean vectors were first tested for difference by a single-classification analysis of dispersion. On the basis of the univariate analysis of variance studies it was expected that the result might be significant, but it was not certain, owing to the preponderance of samples from the Lower Campanian. The analysis was based on samples 1—6. For details concerning the mode of computation the reader is referred to RAO (1952). The value obtained of $V = 172.46$ is highly significant as χ^2 with 24 degrees of freedom and therefore the mean vectors are statistically unlike. It is of interest to ascertain the importance of the contribution of x_2 and x_3 to the statistical difference. This was done by the internal analysis of the set. The method of calculation employed is shown in the following:

Consider the 4×4 matrix

$$\left[\begin{array}{cc:cc} w_{11} & w_{12} & w_{13} & w_{14} \\ \multicolumn{2}{c:}{\mathbf{W}_{11}} & \multicolumn{2}{c}{\mathbf{W}_{12}} \\ w_{21} & w_{22} & w_{23} & w_{24} \\ \hdashline w_{31} & w_{32} & w_{33} & w_{34} \\ \multicolumn{2}{c:}{\mathbf{W}_{21}} & \multicolumn{2}{c}{\mathbf{W}_{22}} \\ w_{41} & w_{42} & w_{43} & w_{44} \end{array}\right]$$

partitioned as shown into 4 submatrices $\mathbf{W}_{11}$, $\mathbf{W}_{12}$, $\mathbf{W}_{21}$, and $\mathbf{W}_{22}$. The following calculations are then made:

1. $\mathbf{W}_{11}^{-1}$.
2. $\mathbf{W}_{21}\mathbf{W}_{11}^{-1}$.
3. $\mathbf{W}_{21}\mathbf{W}_{11}^{-1}\mathbf{W}_{12}$.
4. $\mathbf{W}_{22} - \mathbf{W}_{21}\mathbf{W}_{11}^{-1}\mathbf{W}_{12} = \mathbf{W}(2|2)$.

This given the "within sum of products" matrix for x_3 and x_4, as the situation is in the present case, after extracting for x_1 and x_2. Similarly for $\mathbf{S}$ one obtains

$$\mathbf{S}(2|2) = \mathbf{S}_{22} - \mathbf{S}_{21}\mathbf{S}_{11}^{-1}\mathbf{S}_{12}.$$

From these matrices one calculates the statistic

$$\Lambda = \frac{|\mathbf{W}(2|2)|}{|\mathbf{S}(2|2)|}.$$

From this V is readily found.

The result found of $V = 165.29$ is highly significant as χ^2 with ten degrees of freedom. This means that x_2 and x_3 could be used in conjunction to distinguish between populations without the addition of x_1 and x_4, which is a result of practical importance.

The individual vector differences between samples were tested by the T^2-test. All differences were found to be highly significant except the differences between samples (3) and (5) and samples (4) and (6), for which no significant difference could be demonstrated. The investigation treated the four Campanian and two Santonian homogeneous samples.

Summarizing remarks

The results of the T^2 investigation indicate a generally high degree of unlikeness between samples, even between the Campanian occurrences. The unlikeness between Campanian samples may be a reflection of sorting effects with resultant bias in the study material, whereas the unlikeness between the Santonian and Campanian samples would seem to be due to the trend in size in the dimensions, already noted in the foregoing.

GENERALIZED DISTANCE STUDY

The MAHALANOBIS' generalized distances between samples were computed as part of the work in obtaining T^2. For the method of calculation the reader is referred to RAO (1952). The results obtained for the 6 samples with non-heterogeneous covariance matrices are shown in the following array of values.

Sample	1	2	3	4	5	6
1	0	1.21	6.59	0.95	1.95	1.86
2		0	5.85	0.81	0.84	0.78
3			0	1.10	0.71	1.02
4				0	1.61	0.54
5					0	1.73
6						0

The D-values are based on the four dimensions x_1, x_2, x_3, x_4; they were used in making a topologic lattice model. A drawing of this model is shown in Fig. 15. Each ball in the model represents one of the six localities. A tendency towards clustering is shown only by localities 2, 4, and 6. We return to this topic further on in the present section.

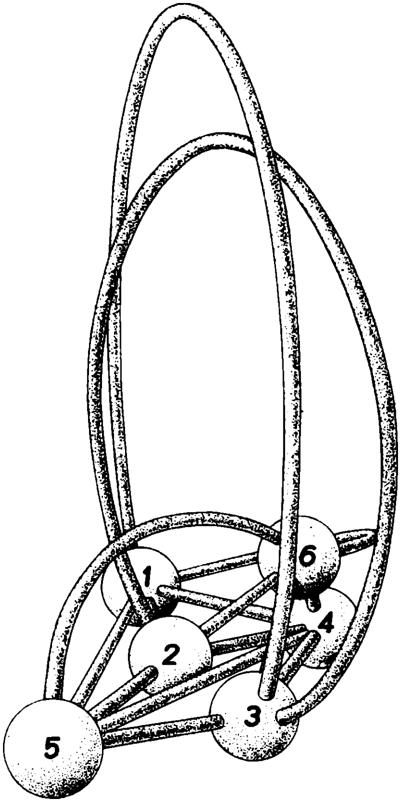

Fig. 15. Three-dimensional model of 15 quadrivariate generalized distances for *Actinocamax verus* s. l.

(1 = Lower Campanian of Djurun; 2 = Lower Campanian of Boguchar; 3 = Santonian of Ulianovsk; 4 = Lower Campanian of Boguchar; 5 = Santonian of Lgov; 6 = Lower Campanian of the River Don near Kazanskaia.)

The method of inverting the 4×4 symmetric matrices found most convenient is outlined below; it is that of inversion by partitioned matrices.

Consider the 4-variate covariance matrix Σ partitioned as shown.

$$\Sigma = \left[\begin{array}{cc:cc} \sigma_{11} & \sigma_{12} & \sigma_{13} & \sigma_{14} \\ \multicolumn{2}{c:}{\Sigma_{11}} & \multicolumn{2}{c}{\Sigma_{12}} \\ \sigma_{21} & \sigma_{22} & \sigma_{23} & \sigma_{24} \\ \hdashline \sigma_{31} & \sigma_{32} & \sigma_{33} & \sigma_{34} \\ \multicolumn{2}{c:}{\Sigma_{21}} & \multicolumn{2}{c}{\Sigma_{22}} \\ \sigma_{41} & \sigma_{42} & \sigma_{43} & \sigma_{44} \end{array}\right].$$

1. The first stage is to invert Σ_{11}.
2. $\Sigma_{11}^{-1}\Sigma_{12}$ and $\Sigma_{21}\Sigma_{11}^{-1}$. A check is provided by the fact that the one matrix is the transpose of the other.

3. $(\boldsymbol{\Sigma}_{21}\ \boldsymbol{\Sigma}_{11}^{-1})\ \boldsymbol{\Sigma}_{12}$.
4. $(\boldsymbol{\Sigma}_{22} - \boldsymbol{\Sigma}_{21}\ \boldsymbol{\Sigma}_{11}^{-1}\ \boldsymbol{\Sigma}_{12})$.
5. Calculate the inverse of 4. This is the lower right hand partitioned matrix of $\boldsymbol{\Sigma}^{-1}$ and it will be denoted by $\mathbf{C}_{22}$.
6. $\mathbf{C}_{21} = -\mathbf{C}_{22}\,\boldsymbol{\Sigma}_{21}\ \boldsymbol{\Sigma}_{11}^{-1}$.
7. $\mathbf{C}_{12} = -\ \boldsymbol{\Sigma}_{11}^{-1}\,\boldsymbol{\Sigma}_{12}\mathbf{C}_{22}$.
8. $\mathbf{C}_{11} = \boldsymbol{\Sigma}_{11}^{-1} - \boldsymbol{\Sigma}_{11}^{-1}\,\boldsymbol{\Sigma}_{12}\mathbf{C}_{21}$.
9. The required inverse is

$$\boldsymbol{\Sigma}^{-1} = \left[\begin{array}{cc:cc} c_{11} & c_{12} & c_{13} & c_{14} \\ \multicolumn{2}{c:}{\mathbf{C}_{11}} & \multicolumn{2}{c}{\mathbf{C}_{12}} \\ c_{21} & c_{22} & c_{23} & c_{24} \\ \hdashline c_{31} & c_{32} & c_{33} & c_{34} \\ \multicolumn{2}{c}{\mathbf{C}_{21}} & \multicolumn{2}{c}{\mathbf{C}_{22}} \\ c_{41} & c_{42} & c_{43} & c_{44} \end{array}\right].$$

For 4×4 symmetric matrices this method of inversion seems to be quick and is also partly self-checking; $\mathbf{C}_{21}$ checks against $\mathbf{C}_{12}$ and $\mathbf{C}_{11}$ must be symmetric. (See FADDEEVA, 1959, p. 102.)

Unfortunately, the method leads to some inaccuracy owing to the large number of multiplications and divisions. A comparison between D-values derived from this method and electronically is shown below.

Electronically computed value of D	1.21	6.59	0.95	1.95	1.86	5.85	0.81	0.84	0.78	1.10	0.71	1.02	1.61	0.54	1.73
Desk calculator value of D	1.89	4.23	2.01	1.08	1.60	5.87	1.10	1.66	0.78	1.74	0.89	1.03	1.61	0.56	1.73

The effect of additional variables on the generalized distance

It is of interest to ascertain whether the statistical distance between populations would be increased by the inclusion of additional variables. The septivariate generalized distance between samples 2 and 4 was therefore found. The matrix inversion was performed by means of program $Q\,3$ on the BESK computer.

The pooled covariance matrix between samples 2 and 4 is as follows $(N_1 + N_2 - 2 = 100)$:

$$\mathbf{S}\omega = \begin{bmatrix} 0.166787 & 0.073741 & 0.024470 & 0.016686 & 0.020903 & 0.012278 & 0.020417 \\ 0.073741 & 0.073597 & 0.010877 & 0.010829 & 0.009177 & 0.003513 & 0.010326 \\ 0.024470 & 0.010877 & 0.004923 & 0.004447 & 0.002595 & 0.001126 & 0.003323 \\ 0.016686 & 0.010829 & 0.004447 & 0.004500 & 0.001394 & 0.001439 & -0.000923 \\ 0.020903 & 0.009177 & 0.002595 & 0.001394 & 0.031700 & 0.018241 & 0.014313 \\ 0.012278 & 0.003513 & 0.001126 & 0.001439 & 0.018241 & 0.009449 & 0.000596 \\ 0.020417 & 0.010326 & 0.003323 & -0.000923 & 0.014313 & -0.000596 & 0.014809 \end{bmatrix},$$

and

$$\mathbf{S}\omega^{-1} = \begin{bmatrix} 9.63 & -0.12 & 53.71 & -97.79 & -25.75 & 44.84 & -14.31 \\ -0.12 & 18.40 & -97.22 & 57.84 & 9.85 & -22.46 & 7.19 \\ 53.71 & -97.22 & -769.70 & 899.92 & 159.90 & -377.39 & 162.62 \\ -97.79 & 57.84 & 899.92 & -519.43 & -94.18 & 251.72 & -119.07 \\ -25.75 & 9.85 & 159.90 & -94.18 & -24.00 & 73.97 & 40.24 \\ 44.84 & -22.46 & -377.39 & 251.72 & 73.97 & -84.25 & -63.63 \\ -14.31 & 7.19 & 162.62 & -119.07 & 40.24 & -63.63 & -9.65 \end{bmatrix}.$$

The difference vector is

$$\bar{\mathbf{d}} = \begin{bmatrix} 2.924 \\ 1.076 \\ 0.532 \\ 0.510 \\ 0.611 \\ 0.204 \\ 0.405 \end{bmatrix}$$

A value of $D^2 = 1.3018$ was obtained, with $D = 1.141$. Hence, little is gained by extending the computations from 4 to 7 variates, the corresponding generalized distance for four variables being 0.81.

Bivariate generalized distance studies

Two-dimensional generalized distance studies were made for the variate pairs x_1, x_2 and x_2, x_3. As indicated already in the chapter on homogeneity of covariance matrices the bivariate covariance matrices for the eight samples of the two variates x_1 and x_2 are all not equal. Despite this fact all eight samples are considered in the construction of a generalized distance model for these two variates. The position for the covariance matrices based on the two variates x_2 and x_3 is that seven could not be shown to be heterogeneous with respect to each other while that of sample 7 is decidedly divergent. It is excluded from the generalized distance study for the variate pair $x_2 - x_3$. The generalized distance model for x_1 and x_2 is shown in Fig. 16:

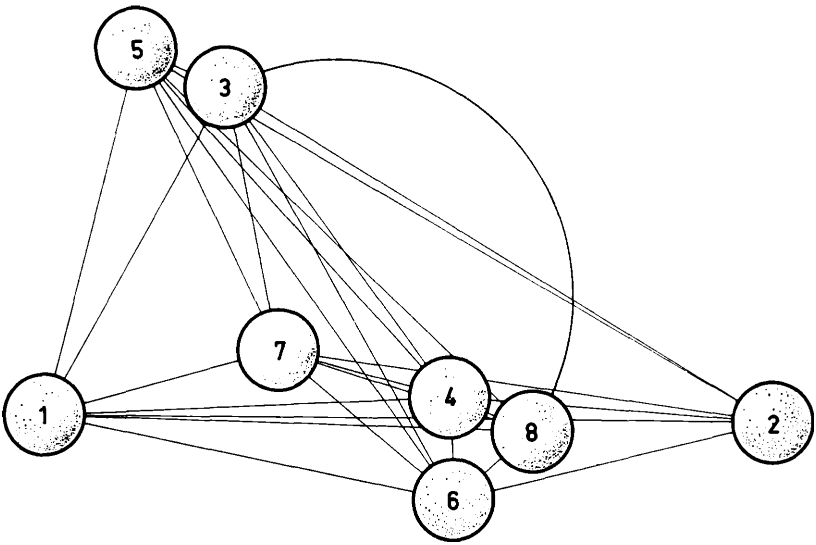

Fig. 16. Two dimensional generalized distance model for eight heterogeneous samples; 1, Lower Campanian; 2, Lower Campanian; 3, Santonian; 4, Lower Campanian; 5, Santonian; 6, Lower Campanian; 7, Upper Coniacian; 8, Lower Campanian. (Dimensions x_1 and x_2.)

This model presents some interesting features that are not directly apparent from the four-dimensional model. We note the clusters formed by 3 and 5 and by 4, 6, and 8. Sample 2 lies near the Campanian 4—6—8 cluster and could be reckoned to it while 7 lies between the Santonian 3—5 cluster and the Campanian cluster. The Lower Campanian "ball" 1 occupies an isolated position.

The generalized distance model for x_2 and x_3 is shown in Fig. 17.

The dimensions x_2 and x_3 are the width and breadth of the belemnite rostrum and may be expected to vary less than the dimension of rostral length, x_1; the section on univariate statistics confirms this supposition as does also the principal component analysis. Consequently, one might expect a somewhat different grouping of the samples on the basis of these two dimensions. Fig. 17 differs from Fig. 16 in several interesting connexions. Firstly, there are two definite Lower Campanian clusters; 4 and 6 cluster closely and 1, 2, and 8 build a cluster. This latter grouping is surprising considering the isolated position of sample 1 in Fig. 16 and in the four-dimensional study. Finally, we have the Santonian 3—5 cluster, which is in this diagram less pronounced than in Fig. 16. Summing up, we have a Campanian cluster at one extreme and a Santonian cluster at the other, with a somewhat anomalous intermediate Campanian cluster. The two extreme positions agree well with what is to be expected remembering that we have established the possibility of a chronocline from early Senonian to late Senonian time. The 4—6 cluster is not so easy to explain but we note that 4 and

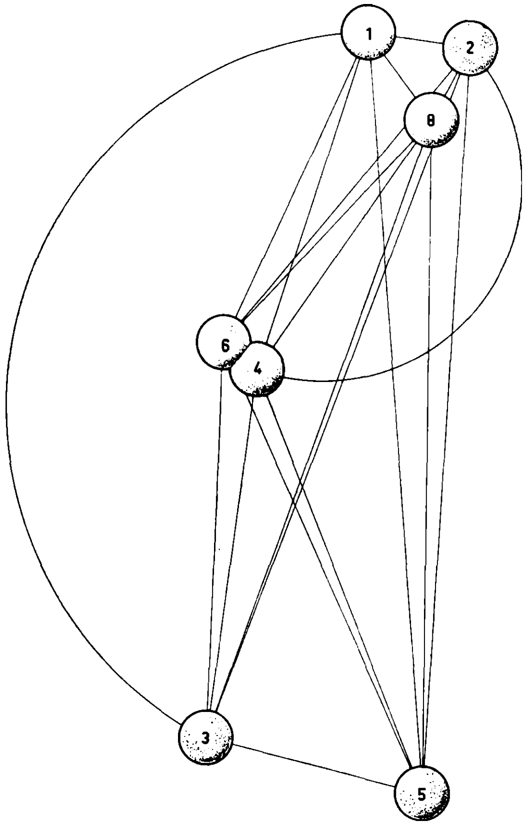

Fig. 17. Two dimensional generalized distance model for seven samples; 1, Lower Campanian; 2, Lower Campanian; 3, Santonian; 4, Lower Campanian; 5, Santonian; 6, Lower Campanian; 8, Lower Campanian. (Dimensions x_2 and x_3).

6 are also intermediary in the model shown in Fig. 16, although in that connexion rather closely grouped with the two Campanian samples 2 and 8.

Summarizing remarks

It will readily be seen that the four-dimensional and two-dimensional topologic models of the *D*-values for *Actinocamax verus* s. l. are distorted. As is discussed by one of us elsewhere (REYMENT, 1962) this is partly due to the nature of the covariance matrices, which are to greater and lesser degrees "unequal", even although the significance level in that respect is not attained. A truly satisfactory *D*-model may only be expected when the respective covariance matrices are truly equal. A second factor which may be considered partly to account for the distortion of the quadrivariate model is the fact that it is a three-dimensional representation of a four-dimensional problem. This, coupled with the state of affairs that x_4 does not seem to be compatible with x_1, x_2, and x_3, would seem to be contributory causes. The introduction of further variables into the calculations could not be shown to improve matters.

Speaking in terms of unlikeness the two most dissimilar quadrivariate samples are samples 2 and 3 (Santonian-Lower Campanian); thereafter we have samples 1 and 3 (Santonian-Lower Campanian). The two closest samples are 4 and 6 (both Lower Campanian) and thereafter the two Santonian samples 3 and 5. The closeness of samples 4 and 6 is also shown by the bivariate model for variates x_2 and x_3 (Fig. 17), but this is less apparent in the other bivariate model (Fig. 16). On the other hand the Santonian samples are close in Fig. 16 but more divergent in Fig. 17. The tendency for values to cluster (RAO, 1949b) is more pronounced in the bivariate models and is probably obscured in the quadrivariate model by distortion.

Both the generalized distance study as well as the T^2-investigation and the analysis of dispersion study bring out the considerable heterogeneity in means between most combinations of samples, even between, for example, some Lower Campanian samples. It has already been demonstrated that the evolution of *Actinocamax verus* s.l. from Lower Coniacian to Lower Campanian time seems to have been accompanied by a general decrease in size dimensions. It is therefore not surprising to see large D-values between Santonian and Lower Campanian samples, but it is, on the surface, unexpected to find relatively large and significant D-values between Lower Campanian samples.

The two-dimensional topologic models indicate more definite clustering than is done by the quadrivariate model. There is a strong tendency to form a Santonian cluster and two Lower Campanian clusters.

The bivariate D-studies thus support the postulation of the existence of a multivariate chronocline with size diminution as a function of time.

It now remains to review the agreement between the groupings indicated by the statistical work and those made on qualitative paleontologic grounds. In the chapter on the paleontologic characterization of the material it was pointed out that *Actinocamax verus* s.l. is in the Russian Platform region represented as an earlier taxonomic entity confined almost entirely to the Coniacian and Santonian, namely, the group of *Actinocamax verus fragilis*. A second group, that of *Actinocamax verus laevigatus*, replaces the *fragilis* group in the Lower Campanian. The biometric results would seem to agree well with these qualitative taxonomic conclusions, bearing in mind the tendency to form a Santonian cluster and the Lower Campanian clusters, the intermediary of which could possibly represent slightly older transitional Lower Campanian material.

DISCRIMINANT FUNCTION STUDY

1. *Classifying Santonian and Campanian specimens.* For the purpose of classifying a specimen as either Santonian or Campanian in age, providing that it has really come from the Santonian or Campanian, the discriminant function between samples 4 and 5 was computed. It is

$$\delta_{45} = -x_1 - 47.869x_2 + 69.548x_3 + 18.024x_4 - 4.362.$$

Its efficiency in classifying an unknown specimen correctly was ascertained by substituting the original measurements in the discriminant function (Campanian < 12.937; Santonian > 12.937). The percentage of wrong classification was found to be about 20 for both Campanian and Santonian. The means of the other 7 samples were substituted in this equation to see how they would classify. Samples 1, 2, 4, 6, and 8 classified as Campanian correctly and samples 3 and 5 classified correctly as Santonian. Sample 9 from the Lower Coniacian classified with the Santonian group and sample 7 from the Upper Coniacian classified with the Campanian group.

2. *Classification of a specimen into one of three populations.* Using the information yielded by the construction of the generalized distance model three of the samples were arbitrarily selected for the construction of discriminant functions suitable for permitting a division of the data into one of three populations. The chosen samples were 1, 2, and 5, of Campanian, Campanian and Santonian age respectively.

The three samples have the following mean vectors

Sample 5 (Santonian) $=\pi_1$		Sample 1 (Campanian) $=\pi_2$	Sample 2 (Campanian) $=\pi_3$
x_1	3.457	3.160	2.799
x_2	0.589	0.515	0.523
x_3	0.581	0.479	0.479
x_4	0.353	0.232	0.235

The inverse of the sums of squares and products matrix is

$$\mathbf{A}^{-1} = \begin{bmatrix} -0.1507 & 1.6422 & -1.3401 & 0.2128 \\ 1.6422 & -6.0405 & 2.6008 & -1.6130 \\ -1.3401 & 2.6008 & 2.7087 & 0.9666 \\ 0.2128 & -1.6130 & 0.9666 & 0.4712 \end{bmatrix}.$$

This matrix is used instead of the covariance matrix for finding the required discriminant functions, these differing from those obtainable from the covariance matrix only by a constant factor $N_1 + N_2 + N_3 - 3$.

The discriminant function between samples from π_1 and π_2:

The difference vector $\bar{\mathbf{x}}^{(1)} - \bar{\mathbf{x}}^{(2)} = \mathbf{d}^{(1)} = (0.297, 0.074, 0.102, 0.121)'$. The discriminant function coefficients $\boldsymbol{\lambda}^{(1)} = \mathbf{A}^{-1}\mathbf{d}^{(1)} = (-0.0342, 0.1108, 0.1877, 0.0995)'$. The required discriminant functions are then

$$\Delta_{12} = -0.0342x_1 + 0.1108x_2 + 0.1877x_3 + 0.0995x_4 - 0.0766$$
$$\Delta_{21} = 0.0342x_1 - 0.1108x_2 - 0.1877x_3 - 0.0995x_4 + 0.0776,$$

where $\frac{1}{2}(\bar{\mathbf{x}}^{(1)} + \bar{\mathbf{x}}^{(2)}) = 0.0766$.

The discriminant function between samples from π_1 and π_3:

The difference vector $\bar{\mathbf{x}}^{(1)} - \bar{\mathbf{x}}^{(3)} = \mathbf{d}^{(2)} = (0.658, 0.066, 0.102, 0.118)'$. The discriminant function coefficients $\boldsymbol{\lambda}^{(2)} = \mathbf{A}^{-1}\mathbf{d}^{(2)} = (-0.1024, 0.7568, -0.3198, 0.1878)'$. The required discriminant functions are then

$$\Delta_{13} = -0.1024x_1 + 0.7568x_2 - 0.3198x_3 + 0.1878x_4 + 0.0138$$
$$\Delta_{31} = 0.1024x_1 - 0.7568x_2 + 0.3198x_3 - 0.1878x_4 - 0.0138,$$

where $\frac{1}{2}(\bar{\mathbf{x}}^{(1)} + \bar{\mathbf{x}}^{(3)}) = -0.0138$.

The discriminant function between samples from π_2 and π_3:

The difference vector $\bar{\mathbf{x}}^{(2)} - \bar{\mathbf{x}}^{(3)} = \mathbf{d}^{(3)} = (0.361, -0.008, 0.000, -0.003)'$. The discriminant function coefficients $\boldsymbol{\lambda}^{(3)} = \mathbf{A}^{-1}\mathbf{d}^{(3)} = (-0.0682, 0.6460, -0.5075, 0.0883)'$. The required discriminant functions are then

$$\Delta_{23} = -0.0682x_1 + 0.6460x_2 - 0.5075x_3 + 0.0883x_4 + 0.0904$$
$$\Delta_{32} = 0.0682x_1 - 0.6460x_2 + 0.5075x_3 - 0.0883x_4 - 0.0904,$$

where $\frac{1}{2}(\bar{\mathbf{x}}^{(2)} + \bar{\mathbf{x}}^{(3)}) = -0.0904$.

Since the *a priori* probabilities are taken to be equal the best regions of classification are. —

$$\pi_1 : \Delta_{12} \geqslant 0 ; \Delta_{13} \geqslant 0$$
$$\pi_2 : \Delta_{21} \geqslant 0 ; \Delta_{23} \geqslant 0$$
$$\pi_3 : \Delta_{31} \geqslant 0 ; \Delta_{32} \geqslant 0.$$

The results obtained will now be used to classify the remaining samples of *Actinocamax* into one of these three regions, which is possible, as long as any sample really does belong to one of these regions.

Sample	age of sample	classification
3	Santonian	with π_1 or π_3 — uncertain
4	L. Campanian	with π_3
6	L. Campanian	with π_3
8	L. Campanian	with π_2

The probabilities of misclassification for the three groups were computed with the aid of Part II of PEARSON's (1931) "Tables for statisticians and biometricians" — tables for volumes of the normal bivariate surface. The probabilities for misclassification of an individual are all high. For individuals from π_1, π_2, and π_3 the probabilities of misclassification are respectively 0.51, 0.64, and 0.49.

EVALUATION OF THE RESULTS AND CONCLUSIONS

The present work is concerned with the biometric study of 237 specimens of *Actinocamax verus* s.l. MILLER, derived from 9 samples of from Lower Coniacian to Lower Campanian age. (In the standard symbols of the Soviet stratigraphers Cn_2, Cn_1, Snt, Cmp_1.) Several significant facts have emerged from the investigation. Perhaps the most striking of these is the occurrence of heterogeneity in the covariance matrices, and even where heterogeneity could not be demonstrated significantly in a set of multivariate samples, there is distortion. As indicated elsewhere by R. A. R. (1962) distortion in biologic covariance matrices may arise in several ways. The first is by virture of morphoevolutionary changes. For example, the covariance matrix $\mathbf{\Sigma}$ changes infinitesimally with respect to time as $\frac{d\mathbf{\Sigma}}{dt}$.

$$\frac{d\mathbf{\Sigma}}{dt} = \begin{bmatrix} \frac{d\sigma_{11}}{dt} & \cdots & \frac{d\sigma_{1p}}{dt} \\ \vdots & & \vdots \\ \frac{d\sigma_{p1}}{dt} & \cdots & \frac{d\sigma_{pp}}{dt} \end{bmatrix}.$$

The distortion arises owing to the fact that these displacements in the elements may be unequal owing to slight, cumulative, phylogenetic, allometric growth changes (REYMENT, 1960 b, p. 7). This type of differential growth distortion is of fundamental biologic importance.

In the present study it would seem that the biologic differences of the kind just mentioned are masked by a second factor. This factor is here interpreted as being due to secondary size sorting in the material; it is known that belemnite rostra may be somewhat susceptible to the effects of water transport (e.g., see HECKER, 1957, pl. 2, fig. 3). Heterogeneity occasioned by sampling from biassed material of the type here under discussion may tend to be more extreme than biologic heterogeneity. In the present study it would therefore seem that there is a definite decrease in the magnitudes of x_1, x_2, and x_3 from Lower Coniacian time to Lower Campanian time; the existence of a multivariate chronocline would seem to be indicated, but this is disturbed and partly obscured by postmortal sorting. In addition hereto we have also the influence of environment effects (cf. RAO, 1960, p. 329). Consequently, every measurement, x_i, will in reality consist of three factors, namely one, a_i, representing the inner, genetic variability of the organism (= that which leads to evolutionary changes), a random variable, δ_i, due to the influence of environment, and a random variable, ε_i, due to postmortal sedimentary processes.

$$x_i = a_i + \delta_i + \varepsilon_i.$$

In the present case of $\varepsilon_i > \delta_i$. The magnitude of ε_i will vary considerable from problem to problem and sample to sample and may even be zero. Its importance may to a certain extent be adjudged from a sedimentologic analysis of the data. The effect of δ_i will vary from species to species, some being morphologically more sensitive to, say, temperature fluctuations than others. The effects of δ_i are at present being studied by R. A. R. for ostracods. One dimension, x_4, would seem to be largely independent of ε_i in that forces operating successfully on x_1, x_2, and x_3 will not greatly influence x_4 (and ϱ_{14}, ϱ_{24}, and ϱ_{34} do not generally differ significantly from zero; also evinced by the results of the principal component analysis).

In the following table the coefficients of variation for x_4 are given for each of samples 1—8.

Sample	1	2	3	4	5	6	7	8
Age	Cmp1	Cmp1	Snt	Cmp1	Snt	Cmp1	Cn2	Cmp1
V	66.90	39.44	38.37	49.75	37.59	44.60	58.38	45.63

Comparison of these values with those for x_1, x_2, and x_3 discloses that fluctuations in V_{x_4} are not accompanied by corresponding fluctuations in the coefficients of variation of the other three variables. Particularly striking is the large coefficient of variation for sample 1, which has low values for the coefficients of variation for x_1, x_2, and x_3. It is here tentatively suggested that x_4 is largely directly independent of ε_i. As indicated by Fig. 12 it may not be particularly associated with the morphoevolutionary changes in x_1, x_2, and x_3; it is possible that it may be mainly influenced by δ_i, the environmental factor. For ease of reference a table of means of x_4 with respect to age for 9 samples is given below.

Age	Cn		Snt		Cmp1				
$\bar{x}_4$	0.200	0.230	0.282	0.353	0.232	0.235	0.204	0.198	0.158

The main computational work in the present investigation was concentrated to the variables x_1, x_2, x_3, and x_4. It should, however, be possible, as suggested by the results of the manova (p. 158) analysis, to obtain good results using x_2 and x_3 on their own. In other words, the breadth and width dimensions are sufficiently different in the populations.

The tests for differences in mean vectors between samples (15 pairs) are informative and would appear to indicate that almost all combinations show significant statistical unlikeness. It should here be brought to mind that belemnite rostra have largely fallen from the drifting carcases of dead animals, or have derived from stranded carcases (REYMENT, 1958). The transport factor ε_i therefore consists of two subfactors, one for the dispersion of the floating carcase (with enclosed rostrum) of short duration, and a second subfactor, almost certainly iterated, for sorting and redeposition of the rostra.

The paleontologic interpretation of the material permits the recognition of two groups on the subspecific level. Firstly, there is the group of *Actinocamax verus fragilis* ARKHANGELSKI, which is mainly confined to the Coniacian and Santonian, but with rare appearances in basal Lower Campanian. This group may be partitioned into *A. verus fragilis* ARKHANGELSKI and *A. v. verus* MILLER by virture of differences in the shape of the rostrum and the nature of the alveolar scar.

The second group is that of *Actinocamax verus laevigatus* ARKHANGELSKI, which is confined to the Lower Campanian. The two subspecific categories *A. verus laevigatiformis* subsp. nov. and *A. verus pseudolaevigatus* subsp. nov. may be broken out of this group.

РЕЗЮМЕ

Настоящая работа посвящена биометрическому изучению 237 экземпляров мелких актинокамаксов. Всего было изучено 9 образцов из коньякских, сантонских и нижнекампанских отложений. В ходе изучения были выявлены интересные факты. Вероятно, наиболее поразительным из них является существование гетерогенности в ковариантных матрицах. Даже в тех случаях, когда гетерогенность не выявляется заметно, в ряду многовариантных образцов наблюдаются искажения.

Как было показано Р. А. РЕЙМЕНТОМ (1962), искажение биологически ковариантных матриц может возникать различными путями.

Первый путь появления искажений возможен при наличии морфоэволюционных изменений. Например, ковариантная матрица $\boldsymbol{\Sigma}$

изменяется бесконечно мало по отношению ко времени, как $\frac{d\mathbf{\Sigma}}{dt}$. то есть

$$\frac{d\mathbf{\Sigma}}{dt} = \begin{bmatrix} \frac{d\sigma_{11}}{dt} & \cdot & \cdot & \frac{d\sigma_{1p}}{dt} \\ \cdot & \cdot & \cdot & \cdot \\ \frac{d\sigma_{p1}}{dt} & \cdot & \cdot & \frac{d\sigma_{pp}}{dt} \end{bmatrix}.$$

Искажение возникает благодаря тому, что смещение элементов может быть неравномерным вследствие слабых совокупных филогенетических аллометрических изменений роста (Р. А. РЕЙМЕНТ, 1960 b, стр. 7). Подобный тип дифференцированного искажения при росте имеет фундаментальное биологическое значение.

В настоящей работе показано, что биологические различия упомянутого типа маскируются другим фактором. Этим фактором, как можно предполагать, является вторичная сортировка материала по величине экземпляров. Хорошо известно, что ростры белемнитов могут переноситься водой (Р. Ф. ГЕККЕР, 1957, табл. 2, фиг. 3). Гетерогенность, обусловленная воздействием подобного фактора, может оказаться более значительной по сравнению с биологической. При проведении настоящего исследования было обнаружено определенное уменьшение значений x_1, x_2 и x_3 [1]) от коньяка к нижнему кампану; выявляется существование мультивариантной хроноклины, но нарушенной и частично замаскированной воздействием посмертной сортировки. В дополнение к этому отмечается влияние среды (С. Р. РАО, 1960, стр. 329). Таким образом каждое измерение x_i в действительности отражает воздействие трех факторов, а именно: α_i — внутренней, присущей организму изменчивости, ведущей к эволюционному изменению; δ_i — случайной изменчивости, обусловленной влиянием среды и ε_i — случайной изменчивости, возникающей в процессе посмертной сортировки.

Следовательно, $x_i = a_i + \delta_i + \varepsilon_i$.

В случае описываемых мелких актинокамаксов $\varepsilon_i > \delta_i$. Величина ε_i может сильно изменяться от образца к образцу и может быть даже равна нулю. Ее значение может быть в определенной степени оценено при седиментационном анализе. Воздействие δ_i может изменяться от образца к образцу. Например, темпера-

[1]) x_1 — длина; x_2 — спинно-брюшной диаметр ростра в месте его вздутия; x_3 — боковой диаметр ростра в том же месте; x_4 — величина альвеолярного излома (см. фиг. 3).

турные колебания на одних образцах проявляются более тонко, чем на других. Воздействие δ_i у остракод в настоящее время изучается Р. А. РЕЙМЕНТОМ.

Наши измерения показали, что величина x_4 в значительной мере не зависит от ε_i, в то время как на x_1, x_2 и x_3, ε_i оказывает значительное воздействие (ϱ_{14}, ϱ_{24} и ϱ_{34} в общем существенно не отличаются от нуля; это же проявляется и в результатах основного компонентного анализа).

В приводимой ниже таблице помещены коэффициенты изменчивости x_4 для образцов №№ 1—8:

№№ образцов	7	3	5	8	6	2	4	1
Возраст	Cn₂	Snt	Snt	Cmp₁	Cmp₁	Cmp₁	Cmp₁	Cmp₁
V	58.38	38.37	37.59	45.63	44.60	39.44	49.75	66.90

Сравнение этих значений со значениями x_1, x_2 и x_3 показывает, что колебания V_{x_4} не сопровождаются соответствующими колебаниями коэффициентов изменчивости трех других переменных. Особенно удивительно но то, что обр. N° 1, который обладает небольшими коэффициентами изменчивости для x_1, x_2 и x_3, характеризуется высоким значением коэффициента x_4. Поэтому предварительно представляется возможным предположить, что x_4 в значительно степени прямо не зависит от ε_i. Как показывает Фиг. 12, величина x_4, в частности, не связана с морфоэволюционными изменениями x_1, x_2 и x_3; возможно, что главное воздействие оказывает фактор окружающей среды δ_i.

Значение x_4 для девяти образцов приведены в следуюей таблице:

Возраст	Cn		Snt		Cmp₁				
$\bar{x}_4$	0.200	0.230	0.282	0.353	0.232	0.235	0.204	0.198	0.158

Основная вычислительная работа в настоящем исследовании была сконцентрирована на переменных x_1, x_2, x_3 и x_4. Однако возможно, как об этом свидетельствуют данные многовараинтного анализа изменения, поиучить хорошие результаты, испобзуя лишь x_2 и x_3. Иными словами, спинно-брюшной и боковой диаметры являются в популяциях достаточно различными.

Исследование различий средних векторов образцов (15 пар) показывает, что почти все комбинации проявляют значительное статистическое несходство.

В этой связи следует иметь в виду, что ростры белемнитов большей частью выпадали из плавающих останков мертвых животных или же вываливались из последних в прибрежной зоне (Р. А. РЕЙМЕНТ, 1958). Фактор переноса ε_i, следовательно, обьединяет две причины: во-первых, рассеивание плавающих останков заключающих ростры в течение непродолжительного времени и, во-вторых, сортировку и переотложение ростров, которые могут повторяться неоднократно.

Несомненно, процессы посмертного разрушения ростра иногда существенным образом сказывались на его внешней форме. Однако все же массовый материал позволяет с достаточной степенью уверенности говорить о возможности разделения по ряду устойчивых признаков мелких актинокамаксов Русской платформы на две группы: группу *Actinocamax verus fragilis* (в основном коньяк-сантон, реже нижняя часть нижнего кампана), состоящую из разнообразных по форме ростра и характеру строения альвеолярного излома *A. verus fragilis* ARKHANGELSKI и *A. verus verus* MILLER и группу *Actinocamax verus laevigatus,* в состав которой входят *A. verus laevigatus* ARKHANGELSKI, *A. verus laevigatiformis* subsp. n., *A. verus pseudolaevigatus* subsp. n.

Перечисленные формы являются географическими и стратиграфическими составляющими вида *Actinocamax verus* MILLER s. l.

REFERENCES

ANDERSON, T. W. 1958. Introduction to multivariate statistical analysis. Wiley & Sons, New York—London, 374 pp.

ARKHANGELSKI, A. D. 1912. Верхнемеловые отложения востока Европейской России. Материалы для геологии России, vol. 25, 333 pp., 10 pls.

BIRKELUND, T. 1957. Upper Cretaceous belemnites from Denmark. Biol. Skr. Danske Vid. Selsk., vol. 9, no. 1, 70 pp., 6 pls.

BLACKITH, R. E. 1961. Multivariate statistical methods in human biology. Med. Dok., vol. 5, no. 2, pp. 26—28.

DAVID, F. N. 1938. Tables of the correlation coefficient. Pub. Biometrika Office, Cambr. Univ. Press, xxxix+55 pp., 4 charts.

FADDEEVA, V. N. 1959. Computational methods of linear algebra. Dover Publications, New York, 252 pp.

FELLER, W. 1950. An introduction to probability theory and its applications. Wiley & Sons, New York—London, 461 pp.

HECKER, R. F. 1957. Введение в палеоэкологию. "Госгеолтехиздат", Moscow, 83 pp., 20 pls.

MAYR, E., LINSLEY, E. G., and USINGER, R. L. 1953. Methods and principles of Systematic Zoology. McGraw-Hill, New York, 328 pp.
MILLER, J. S. 1823. Observations on the genus *Actinocamax.* Trans. geol. Soc. London, ser. 2, vol. 2, pt. 6, pp. 63—67, 1 pl.
MOBERG, C. J. 1885. Cephalopoderna i Sveriges kritsystem. Sver. geol. Unders., ser. C, no. 73, 67 pp., 6 pls.
NAIDIN, D. P. 1952. Верхнемеловые белемниты Западной Украйны. Труд. Моск. Геол. Развед. Инст., vol. 27, pp. 1—125, 21 pls.
— 1959. On the paleogeography of the Russian Platform during the Upper Cretaceous Epoch. Stockh. Contr. Geol., vol. 3, no. 6, pp. 127—138.
— 1960. The stratigraphy of the Upper Cretaceous of the Russian Platform. Stockh. Contr. Geol., vol. 6, no. 4, pp. 39—61.
OLSON, E. C. and MILLER, R. L. 1958. Morphological Integration. Chicago Univ. Press, 317 pp.
PEARSON, K. P. 1931. Editor. Tables for statisticians and biometricians. Part II, Cambridge University Press, 262 pp.
RAO, C. RADHAKRISHNA. 1949 a. On the distance between two populations. Sankhya, vol. 9, pt. 3, pp. 246—248.
— 1949 b. On some problems arising out of discrimination with multiple characters. Sankhya, vol. 9, pt. 3, pp. 343—366.
— 1952. Advanced statistical methods in biometric research. Wiley & Sons, New York—London, 390 pp.
— 1960. Multivariate analysis: an indispensible statistical aid in applied research. Sankhya, vol. 22, pp. 317—338.
REYMENT, R. A. 1958. Some factors in the distribution of fossil cephalopods. Stockh. Contr. Geol., vol. 1, pt. 6, pp. 97—184, 7 pls.
— 1960 a. Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda. Stockh. Contr. Geol., vol. 7, 238 pp., 23 pls.
— 1960 b. Notes on the study of evolutionary changes in ostracods. Rep. 21st Int. geol. Congr., Copenhagen, sect. 6, pp. 7—17.
— 1961. Quadrivariate principal component analysis of *Globigerina yeguaensis.* Stockh. Contr. Geol., vol. 8, no. 5, pp. 17—26.
— 1962. Homogeneity of covariance matrices in paleontologic biometry. Biometrics, vol. 18, pp. 1—11.
SCHLÜTER, C. 1876—1877. Cephalopoden der oberen deutschen Kreide; II Teil. Palaeontographica, vol. 24, pp. 121—263, 20 pls.
STOLLEY, E. 1897. Über die Gliederung des norddeutschen und baltischen Senon, sowie die dasselbe charakterisirenden Belemniten. Arch. Anthrop. Geol. Schlesw.-Holsteins, vol. 2, pt. 2, pp. 216—302, 4 pls.
TERENTIEV, P. V. 1960. Дальнейшее развитие метода корреляционных плеяд. Применение математических методов в биологии. Второе Биометр. Совещание СССР. Изд. Ленингр., Универс., pp. 27—36.

Received June 2, 1961

Printed December 15, 1962, by Ekenäs Tryckeri Aktiebolag, Finland

Price 14.00 Sw. kr

EKENÄS 1962. EKENÄS TRYCKERI AKTIEBOLAG