VARIATION IN *STROMATOCERIUM* AT OUREAU RIVER QUEBEC

by

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A STUDY OF VARIATION IN STROMATOCERIUM IN THE UPPER BLACK RIVER LIMESTONE AT OUAREAU RIVER, QUEBEC

by

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ABSTRACT

The stromatoporoids grew on lime muds in a quiet, shallow water, shelf environment. From the orientation of orthoceracone cephalopods, the current direction was from the east-southeast or the west-northwest or the north-northeast.

The use of the coefficient of variation is invalid in palaeontological studies. Student's 't' can be used to measure variability and is used to show that only one species is present.

Student's 't' tests on twelve parameters in vertical section show that differences between latilaminae are not due to chance and that four parameters are, to a degree, representative of a small group of individuals from one sample station. These parameters, which are the most useful in defining the species, are:

1) width of the broad cyst plates,
2) total number of cyst plates per 4 mm.,
3) number of pillars per 4 mm.,
4) length of pillars.

The holotype is generally atypical of the population. Taxonomic definition based on measurements from one latilamina or a small number of samples is invalid and the type of the species should be a large collection.

The mean values of parameters 2, 3 and 4 above, show a linear correlation with geographic distance which may be related to current direction and indicates that the stromatoporoids are in place. The method may be applicable to other taxa.

The study is based on about 5,250 measurements from 50 individuals.

INTRODUCTION

PURPOSE

During the fall of 1965 a large collection of the stromatoporoid Stromatocerium rugosum was made from a bed, five inches thick, in the Leray Formation of the Black River Group, at the Ouareau river, north-northeast of Montreal, Quebec.

The purpose of the study is to determine whether any measurable parameters in the coenosteum of S. rugosum can be shown to be of palaeoecological significance. The variability of the species, and the relation of the holotype to this variability is described and discussed.

ACKNOWLEDGMENTS

I am indebted to Professor C.W. Stearn for suggesting the problem and for his encouragement and advice throughout this study.

I also wish to thank Dr J. Stanley for his helpful discussions of the statistical methods, and Dr N.D. Newell of the American Museum of Natural History, New York, who made available the thin sections of the holotype.

I am grateful to the Ministère des Richesses Naturelles, Quebec for permission to use unpublished manuscripts prepared by Dr T.H. Clark.

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REPOSITORY

The specimens and thin sections used in the study are in the McGill University Stromatoporoid Collection (catalogue numbers 82-1 to 82-140).

The statistical results and I.B.M. punch cards are housed with the specimens.

PREVIOUS WORK

All previous studies of stromatoporoid palaeoecology have dealt with gross morphology of the coenosteum. Three basic types have been recognised:

1) massive, including subspherical, nodular, mushroom-shaped and dome-like forms,
2) tabular, or plate-like,
3) dendroid.

The stromatoporoids of the Oureau river are of the massive type.

In 1918, Dehorne stated, that by analogy with living reef corals, massive stromatoporoids seemed to have lived in agitated, shallow water near the surface, while dendroid forms were inhabitants of calmer, deeper water. Again in 1920, she affirmed by analogy with living hydrozoans having stony skeletons and commonly associated with hermatypic corals and rudists, that stromatoporoids were essentially organisms of shallow, warm, tropical seas. Living stony hydrozoans, such as Millepora, have massive nodular growth-forms in shallow, agitated water and dendroid, in quiet water; similar growth forms in stromatoporoids probably indicate similar environments.

Lecompte (1951) states in his "Conclusions ecologiques" that stromatoporoids were less suited to clastic environments than corals, being practically absent from shaly or sandy beds. Coral bioherms of Frasnian age were not suitable for stromatoporoids, and inversely, tabulate and rugose corals are rare in stromatoporoid biostromes, indicating that the two groups were adjusted to different situations. He concludes (Lecompte 1954) that, in general terms, reefs of massive stromatoporoids were built above wave base while reefs of tabulate and rugose corals were built below wave base.

Manten (1963) points out that Lecompte's interpretation of waning importance of stromatoporoids with depth in the Belgian Frasnian reefs is open to question. Lecompte's own publications indicate that mud tolerance was a factor of great influence. Lecompte (1951) described how stromatoporoids are abundant in limestones, seldom found in shales and are more affected by mud than corals. The observation that stromatoporoids were intolerant of mud was repeated in 1954. In the Niagaran of Illinois, stromatoporoids decrease in importance as reef builders, as muddy impurities increase (Lowenstam 1950). Thus it is possible that mud tolerance, rather than depth, determined the occurence of stromatoporoids. An increase in the fine fraction of a sediment may be correlated with depth, but not necessarily.

Klovan (1963) generalises that massive stromatoporoids indicate shallow water, turbulent conditions of deposition, while tabular stromatoporoids indicate deeper and quieter water. He points out that some of the limestones of the Redwater Reef Complex of Alberta, containing massive stromatoporoids, are of high argillaceous content. He suggests that possibly this fine matter was trapped between the heads, which served as baffles or that the stromatoporoids were removed from their growth position to an area of quiet-water conditions. Plate-like forms apparently did not require a hard substratum on which to grow. Dendroid forms, such as Stachyodes lived in turbulent as well as moderately turbulent water.

No study of the palaeoecology of stromatoporoids based on their internal structural elements has been published.

Galloway and St. Jean (1955) describe the holotype of Stromatocerium rugosum Hall and figure sections they cut from the type specimen from Watertown, New York, which was collected by James Hall in 1847. They have also published an account of the Ordovician Stromatoporoidea of North America (Galloway and St. Jean 1961).

LOCATION AND DESCRIPTION OF THE AREA

The bed is located about 40 miles north-northeast of Montreal, Quebec. The upper bedding plane is exposed over an area of 550 square yards, on the left bank of the Ouareau river, upstream from the bridge where highway 41 crosses the river, and immediately downstream of the old mill (figs. 1 and 2).

The bed is a fossiliferous, pelletoidal limestone containing abundant specimens of Stromatocerium rugosum. The specimens are in such abundance (plate 1, fig. 1) that the bed is well suited to this type of study.

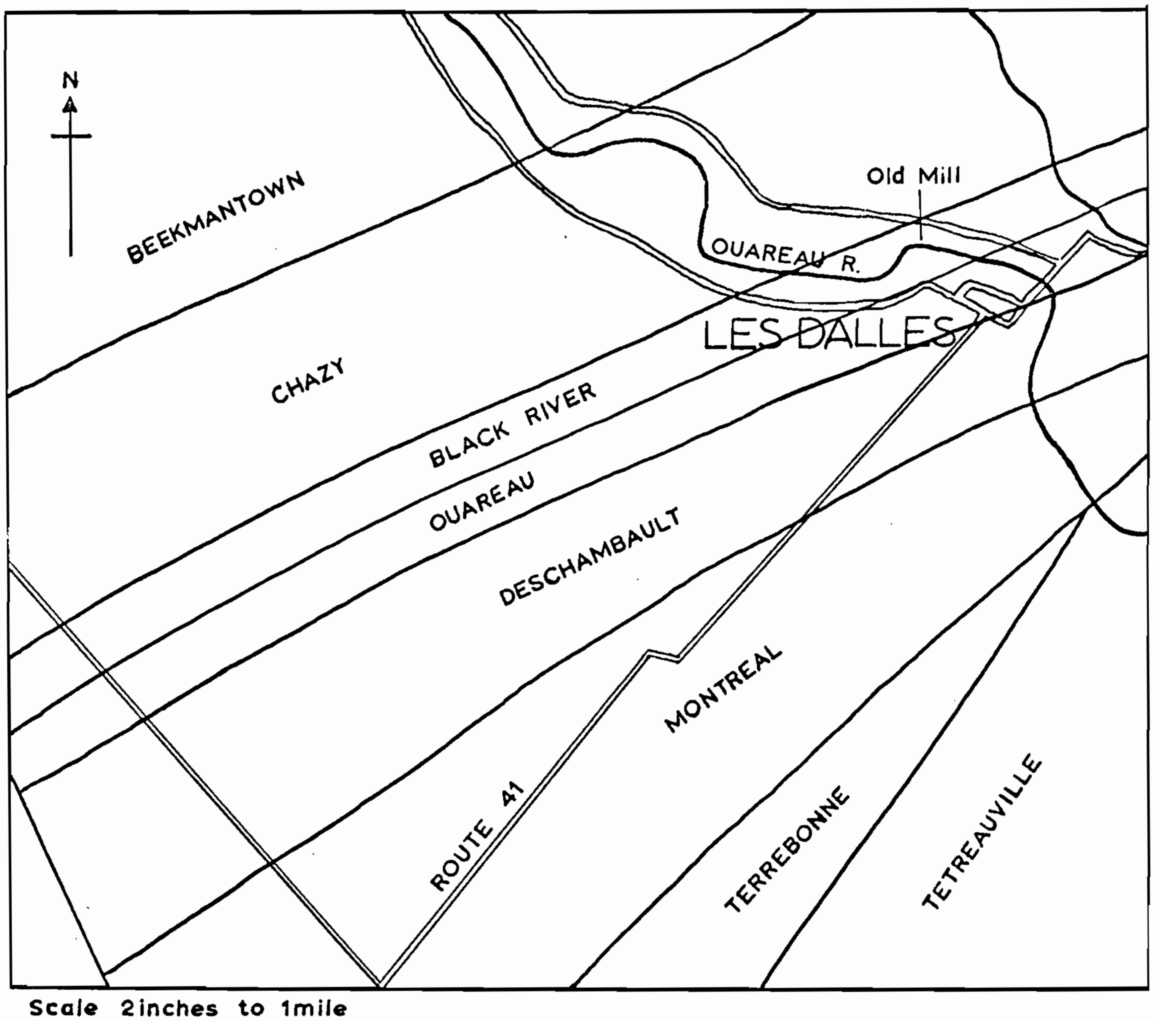
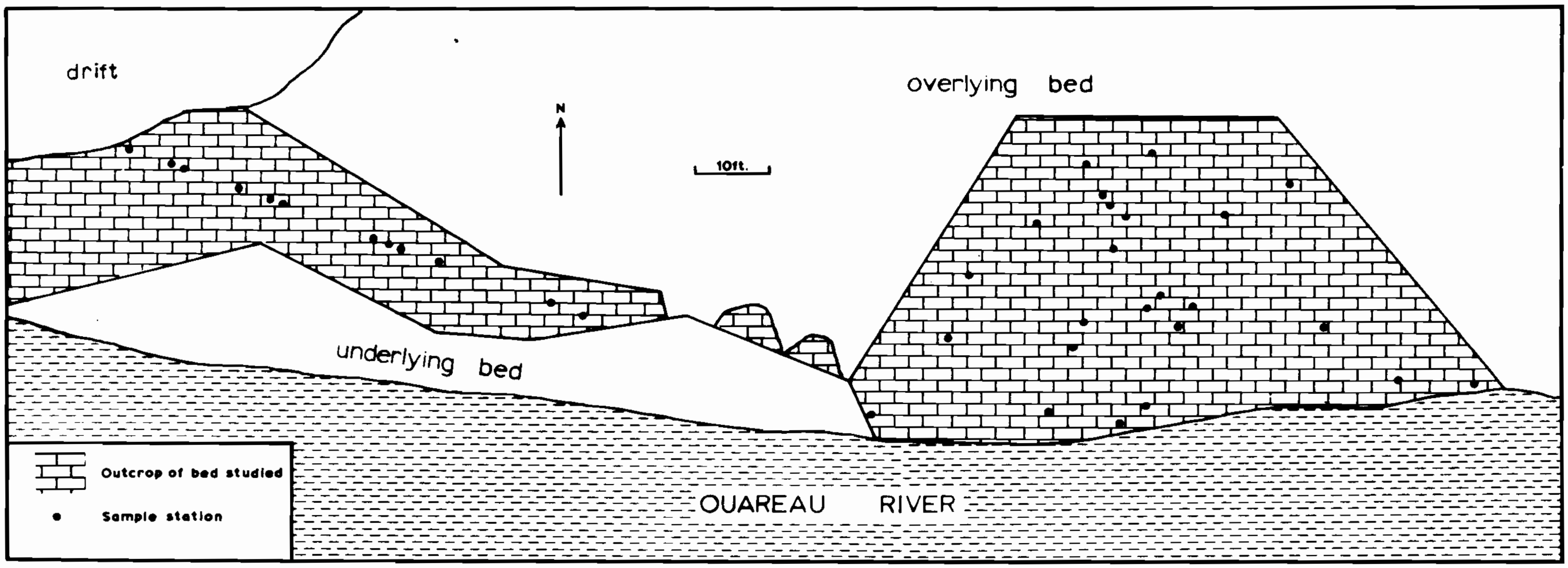


Fig. 1: Geological setting and location of the area.

Fig. 2: Outcrop area of the bed and sample stations used.



GENERAL GEOLOGICAL SETTING

Areal Geology

The area lies in the St. Lawrence Lowlands to the south of the Precambrian rocks of the Laurentian Hills. The lower Palaeozoic sediments have an average dip of 2° to the southeast. In the outcrop above the bridge, the Black River and Trenton Limestones are exposed. The general succession in the area is shown in figure 3.

Ouareau River Section

The rocks exposed in the section range from the Pamelia Formation to the Deschambault Formation. Leray limestones are exposed between the ruins of the old mill and the highway bridge. The upper bedding plane of the bed under study forms a large river flat immediately downstream from the old mill.

TYPE GREAT BRITAIN	
	UPPER ORDOVICIAN
	CARADOC
	MIDDLE ORDOVICIAN
SERIES	MOHAWKIAN

GRAPTOLITE FAUNIZONES	Nemagraptus gracilis	Climacograptus bicornis	Orthograptus truncatus var. intermedius	Orthograptus quadrimucronatus	
STAGE	Porterfield	Wilderness	Barneveld	Eden	
GROUP	Chazy	Black River	Trenton		

FORMATION	PAMELIA	LOWVILLE	LERAY	OUAREAU	DESCHAMBAULT	MONTREAL	TETREAUVILLE including TERREBONNE
THICKNESS IN FEET	10+	8	31	16	92	53+	227

Fig. 3: General succession.

PETROGRAPHY AND PALAEOENVIRONMENT

PETROGRAPHY

One hundred and fifty thin sections show no systematic variation in lithology across the exposed part of the bed. The stromatoporoids rest in all positions of orientation on pelletoidal limestones. The limestone surrounding the stromatoporoids ranges from a fossiliferous pelsparite to a biopelsparite (Folk 1959) and is similar to the lower part of the overlying bed.

The Lower Part of the Bed

The stromatoporoids rest on medium to dark, blue-grey limestone, which weathers buff to rust brown in colour with a mottled appearance. The lower bedding plane is somewhat undulose and the upper surface of this part of the bed is very irregularly undulose.

In thin section, this part of the bed is composed of:

pellets	65%
fossils	15%
oncoliths and other algal structures	10%
sparry calcite cement	10%

The pellets have a uniform size of 0.1 to 0.15 mm., a roundness of 0.9 and a sphericity of 0.9, and are considered to be of fecal origin.

The fauna consists of brachiopods, bryozoans, crinoid ossicles and plates. The bryozoa are excellent geopetal fabrics, for they are filled with pellets at the base and secondary sparry calcite at the top. The surface between the pellets and calcite is parallel to the bedding, suggesting that deposition took place on a nearly horizontal surface.

The oncoliths are possibly algal circumcrustations (Wolf 1962) on pellets, crinoid ossicles and small brachiopod fragments. Algal encrustations are present on many of the faunal elements.

If the pellets are of fecal origin, their abundance suggests a considerable reworking of the sediment, possibly by burrowing organisms. A rounded oval area in one section is probably a burrow, which has been infilled in three stages:

1) by pellets in the base,

2) by a very fine transluscent micrite over the pellets,

3) by secondary spar in the narrow void space at the top.

The cement between the pellets is sparry calcite. The pellets are in contact and therefore the rock could be classified as "grain supported" (Dunham 1962). Compaction has resulted in a coalescing of the pellets in places to give a grumous texture, but this rarely involves more than about five pellets.

The Upper Part of the Bed

The limestone surrounding and overlying the stromatoporoids consists of a highly pelleted lime mud containing an abundant assemblage of brachiopods, gastropods, crinoid ossicles and plates, bryozoans, corals, ostracods, trilobites and orthoceracone cephalopods. Two phases are distinguished:

1) very densely pelletoid with relatively few fossils:

pellets 80%

fossils 15%

spar cement 5%

2) less densely pelletoid areas, round to oval in section:

pellets 20%

fossils 70%

spar cement 10%

Algal encrustations are present in both phases.

The sediment included between the stromatoporoid latilaminae is different from the surrounding rock only in the general absence of a rich fauna. The upper boundaries of the latilaminae are generally sharp and clearly defined. The lower boundaries are more irregular, because the stromatoporoid grew sporadically in the early stages. The following sequence of events is suggested:

1) growth of the stromatoporoid latilamina,

2) latilamina covered by a thin coating of lime mud, and/or pellets,

3) lime mud pelleted,some pellets infiltrating the upper cysts of the latilamina,

4) growth of the stromatoporoid resumed to form the next latilamina.

PALAEOENVIRONMENT

The bed was deposited in a shallow shelf sea in tropical latitudes. The fauna and large amount of lime mud indicate a tropical environment.

Massive stromatoporoids, like those of the Ouareau river, have been assigned by other writers (Dehorne 1918, Lecompte 1954, Klovan 1963) to a high energy environment. The random orientation of the stromatoporoids suggests that they have been transported into the area, possibly from a nearby reef. However, the strong currents required would result in a banking up of the stromatoporoids and a high degree of brecciation of the faunal elements. Neither of these features are observed. Strong currents would also prohibit the deposition of lime muds. Therefore, the stromatoporoids must have grown where they now lie or within a short distance of it.

The latilaminae of stromatoporoids possibly represent stages in growth. Galloway and St. Jean (1955) consider that the latilaminae may correlate with the summer growth season. The average length of the growth season in tropical latitudes is eight months. There is an average of six latilaminae per stromatoporoid. If one latilamina represents one growth season, the average life of a coenosteum would be six years.

A number of orthoceracone cephalopods are exposed with their long axes in the plane of the bed. The azimuth of the adapical end of the shell of 35 individuals was measured. A plot of these measurements (fig. 4) shows a strong preffered orientation and the vector mean to be 209°.

Current action orientates orthoceracone cephalopods with their apices in an upcurrent direction (Kay 1945, Krinsley 1960). They may also be orientated normal to the current direction. Kay (1945) considers that orientation normal to, or parallel to the current direction is a function of size.

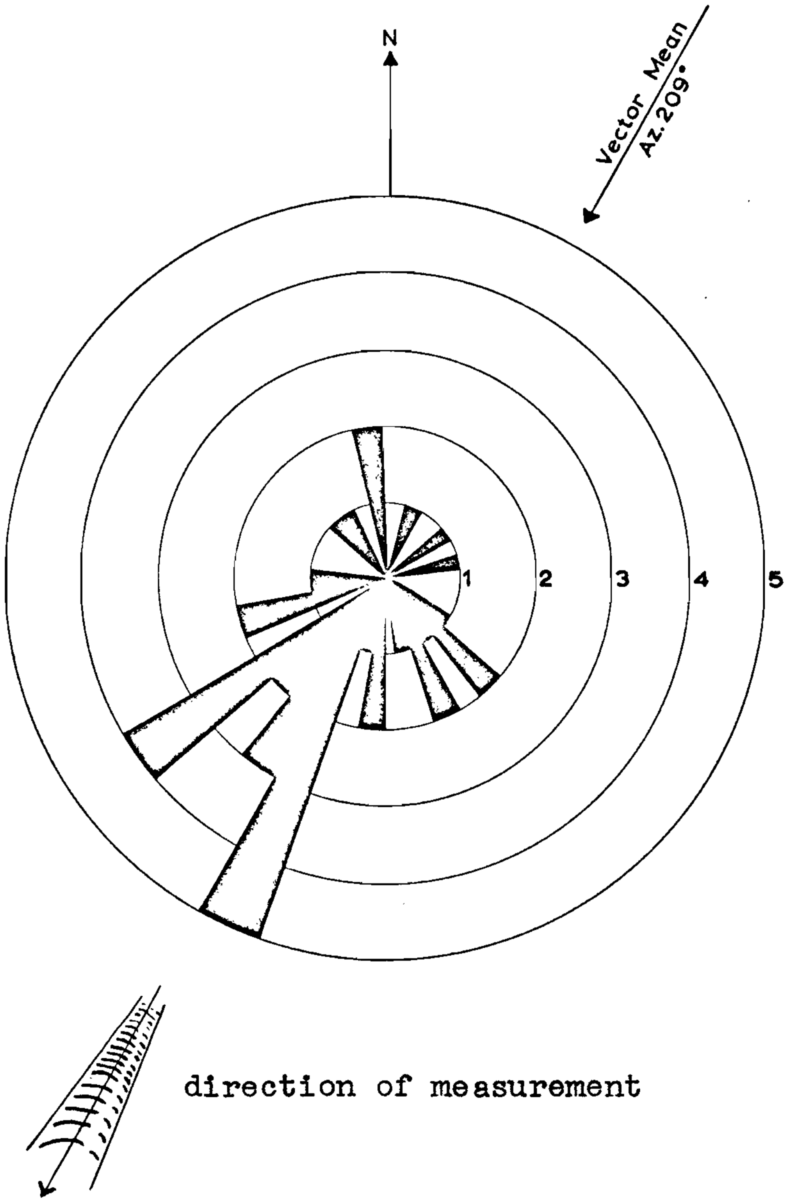


Fig. 4: Orientation of orthoceracone cephalopods.

From this evidence, three current directions are possible:

1) orientation normal to the current

a) current from 119° i.e. ESE.

or b) current from 299° i.e. WNW.

or 2) orientation parallel to the current

a) current from 29° i.e. NNE.

In summary, the environment was probably one of a quiet, shallow carbonate shelf, with conditions suited to the formation and deposition of lime muds and growth of stromatoporoids. The prevailing current direction was from the east-southeast, west-northwest, or north-northeast.

FIELD PROCEEDURES

The exposed bedding plane was initially marked out with three traverse lines "A", "B" and "C": "A" trends 110°, "B", 20° and "C", 155°. Sample points were marked at five foot intervals along these lines. However, the level of the river rose after the initial survey, and the eastern part of traverse "A" had to be moved northwards and was then called "Ax". Samples were taken, where possible, from an area of one square foot at each of the sample points. Further samples were obtained from the areas between the traverses on a random basis. Specimens are identified by a letter corresponding to the traverse. Random samples have the suffix "R".

The process of sampling presented a problem, as the upper bedding plane is smooth. A portable hand saw (Black and Decker, B-230, 7¼ inch) fitted with a silicon carbide abrasive disc and powered by a portable, gasoline-driven generator was used. The intention was to cut samples from the bed. However, the saw proved to be of limited use only. For all but the softest rocks, a diamond blade is necessary, in which case, a water cooling system must be devised. Sampling was therefore carried out mainly with sledge hammers and wedges.

Not all the samples collected were well enough preserved to allow detailed measurements to be taken and not all the sample stations contained stromatoporoids. Of the original sample stations, from which about 150 individuals were collected, 36 sample stations and 50 individuals were used in the study.

STROMATOCERIUM RUGOSUM (HALL)

DESCRIPTION OF THE HOLOTYPE

Galloway and St. Jean (1955) describe the holotype: "......In vertical thin section, the skeleton consists mainly of broad cyst plates, which might be mistaken for laminae, some short, arcuate cyst plates, and long, vertical pillars. The broad cyst plates are from 2 to 5 mm. broad, nearly flat, but are shown to be cyst plates rather than laminae, for they come down to the underlying cyst plates at the ends, and the cysts on two sides of the pillars therefore frequently do not match. There are also narrow arcuate cyst plates 0.25 to 0.5 mm. broad. The cyst plates are close together vertically, 15 to 20 in 4 mm. The cyst plates are tripartite, the median plate 0.25 mm. thick, originally compact but now composed of clear, granular calcite; the upper cyst plate is dark, granular and flocculant, and about as thick as the median plate; the lower cyst plate is dark, granular and flocculant next to the median plate, and about as thick, and is continued downward by a very thick, clear granular, and flocculant layer which is easily overlooked......" (p. 8 and 9).

"The pillars are long, extending through one or several latilaminae; they are irregular in distribution, varying from 4 to 12 in 4 mm. They are narrow or broad, depending on the direction in which they are cut; where cut through the thin part of the pillar, as most pillars are cut, they have a thickness of 0.12 to 0.3 mm., and when cut the broad way the breadth runs up to 0.5 mm. or more.....The pillars consist of a median zone of light-coloured, finely granular calcite, the infiltrated and recrystallised original material, and an outer thin zone of dark, granular, and flocculant tissue, in appearance like the upper and lower layers of the cyst plates. The median cyst plate in some places joins the median zone of the pillars. We consider it most unlikely that the pillars or median cyst plates were ever hollow......" (p. 9 and 10).

"Horizon and Localities: *Stromatocerium rugosum* occurs in the middle Ordovician, Black River Limestone, of Watertown, New York. It also occurs in rocks of the same age at Chazy, New York: Isle La Motte, Vermont: Button Bay Island, off Ferrisburg, Vermont: at Paquette Rapids, Ontario: and in the Ridley Limestone, Wilson County, Tennessee. The species is a good index fossil for the Black River stage. Identifications from other localities and horizons should be checked.

Holotype in the American Museum of Natural History (A.M.N.H. No. 590/5), with eight thin sections, designated 590/5 A to H". (p. 11).

STRUCTURES AND METHODS OF MEASUREMENT

Only vertical sections were used, because making accurate measurements in tangential section was difficult.

Cyst Plates

There are two basic types of cyst plate:

1) broad cyst plates

2) arcuate cyst plates

Both types of cyst plate are illustrated in plate 1, fig. 2.

The broad cyst plates were measured by visual comparison with a chart (fig. 5). The image of the cyst plate was superimposed on the chart by a Zeiss Drawing Apparatus attached to the microscope. Two measurements per cyst were taken:

1) width (D) - see chart fig. 5,

2) radius (r) - see chart fig. 5,

The measurement taken of the arcuate cyst plates was the radius 'R'. This is a measure of the curvature of the arc. This measurement was discontinued, because of the high operator error involved.

Each cyst plate in a vertical traverse across the section was measured in each individual.

The cyst plates are tripartite (plate 1, fig. 3). The median layer of the cyst plate, composed of clear, granular calcite in the holotype, is narrow and dense. The upper layer of the cyst plate, not always present, is wider and less dense than the median cyst plate. The lower layer of the cyst plate is generally the widest and of similar appearance to the upper layer.

Only in parts of a few individuals are the three layers of the cyst plates similar to those of the holotype in appearance. In these specimens, the outer dense layers of the cyst plates are continuous with the outer dense layer of the pillars, (see below), and the inner layer of the cyst plates is continuous with the inner layer of the pillar (plate 2, fig. 1). The less dense layers of the cyst plates are probably

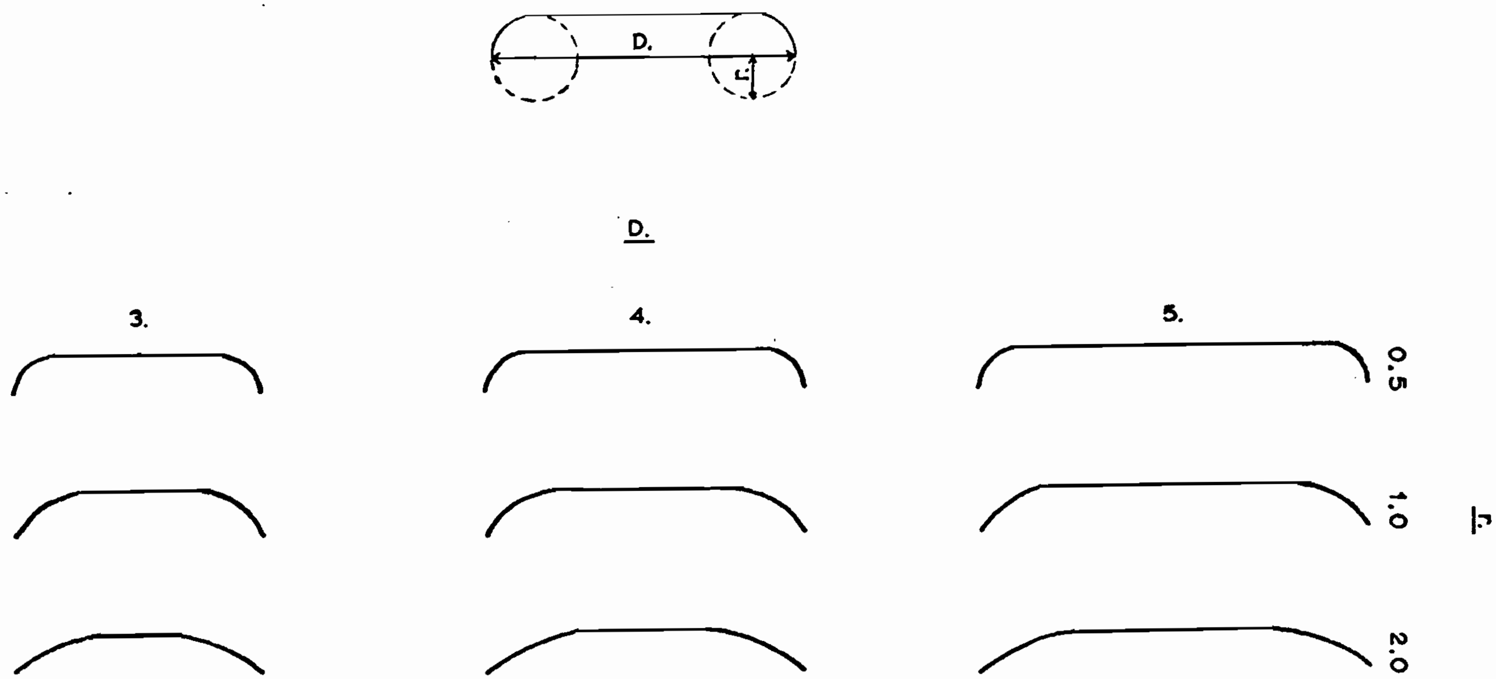


Fig. 5: Chart for the visual comparison of broad cyst plates.

of secondary origin and due to recrystallisation.

The outer margins of the upper and lower layers of the cyst plates are irregular. Measurements were taken from the outer limits of the irregularities. Two measurements were made with a micrometer eyepiece:

1) the total thickness of the cyst plate,
2) the thickness of the lower layer of the cyst plate.

The ratio of the thickness of the lower layer of the cyst plate to the total thickness was calculated. A total of 15, randomly selected, cyst plates in each individual were measured.

The number of broad cyst plates and arcuate cyst plates per 4 mm. vertically was recorded, as was the total number of cyst plates per 4 mm. In each case, 12 to 15 measurements were made.

Pillars

In the holotype, the thickness of the pillars is variable and is dependant on the direction in which the section is cut. This is because the pillars are "....broad and thin, vermicular, curved, branched and have short, spine-like flanges" (Galloway and St. Jean 1955).

The Ouareau river specimens have pillars which vary from being similar to the type, to rod-like and slightly vermicular (0.1 mm. wide and up to 1 mm. long), to round and subround. There are no changes in the vertical sections that can be correlated with those in tangential section.

Three measurements were made:

1) the thickness of the pillars,

2) the length of the pillars,

3) the number of pillars per 4 mm.

Ten measurements per individual were taken for each of the above three values.

Galloway and St, Jean (1955) describe the structure of the pillars in the holotype (see above). In most of the individuals studied, the pillars consist of a median zone of granular calcite and a narrow outer zone of dense material (plate 2, fig. 1). This outer zone has the same appearance as the median layer of the cyst plates. The outer zone of the pillar and the median layer of the cyst plate are commonly continuous (plate 2, fig. 1).

In a few, well preserved individuals, the pillars consist only of dense material. In these individuals, some of the cyst plates are continuous across the pillars (plate 2, fig. 2).

Nestor (1964) interpreted the pillars of Stromatocerium as hollow and developed by supposed upturnings of the laminae or cysts. Galloway and St. Jean (1961) interpret the layers of the cyst plates and pillars as part of the original coenosteum.

From the above evidence, however, it is considered that the pillars were originally composed of dense material, which, in most cases has recrystallised to form an axial zone of granular calcite. In some individuals, the pillars have been completely recrystallised and are now composed of clear granular calcite. It is not thought that the pillars were ever hollow as suggested by Nestor (1964). This contention is supported by Stearn (1966).

About 5,250 measurements were taken during the course of the study.

STATISTICAL ANALYSIS

INTRODUCTION

It is assumed that the samples are representative of the total stromatoporoid population of the exposed part of the bed and also, that the measurements taken are representative of the individual.

There should be no real difference between the latilaminae of an individual. An attempt is made, therefore, to determine which parameters indicate that the difference between the latilaminae of one individual has arisen by chance.

A further assumption is made that the samples from one sample station are of the same species. An attempt is made to determine which parameters have mean values characteristic of the group of individuals at a sample station.

Initially, therefore, it is necessary to determine which parameters indicate that:

1) the difference between the latilamiae of one individual has arisen purely by chance,
2) the difference between a number of samples from one sample station has arisen purely by chance.

Coefficient of Variation

The formula for the coefficient of variation was originally proposed by Karl Pearson (1857-1936), the English leader in biometrics. It is a measure of biological variability based on the relation of absolute dispersion to the mean. It is in every case a good measure of relative dispersion, but relative dispersion is not always a good measure of variability.

Relative dispersion is, however, usually a good measure of variability. The coefficient of variation is regarded as the most useful measure of biological variability that has yet been proposed (Simpson, Roe and Lewontin 1960). The formula is:

$$V = \frac{100S}{\bar{X}}$$

where: V - the coefficient of variation,

S - the standard deviation,

$\bar{X}$ - the mean value of the variate.

"The valid use of 'V' depends on the assumption that variation as a biological function, is relative to absolute size or, in terms of distributions, that absolute dispersion increases in direct proportion to the mean in variates of essentially the same variability from a biological point of view." (Simpson, Roe and Lewontin 1960, p. 90).

In order to test the valid use of 'V', one individual was selected and the coefficients of variation, for each parameter, were calculated:

1) for three latilaminae in one individual,

2) for sections of the same latilamina within the individual.

The coefficients of variation are given in tables 1 and 2 respectively.

In modern, homogenous populations, the values of the coefficient of variation should be between 4 and 10. Average values are 5 and 6. Values lower than 4 indicate that the sample is not large enough, and values higher than 10 indicate that the sample was not pure; for example, individuals of

	A50/B/1	A50/B/2
Width of broad cyst plates	8.764	5.709
Radius of broad cyst plates	5.493	7.549
Radius of arcuate cyst plates	10.861	103.267
Number of cyst plates per 4 mm:		
1) broad	1.637	3.22
2) arcuate	9.09	37.796
3) total	1.264	4.56
Number of pillars per 4 mm.	5.459	4.477
Thickness of the pillars	0.01	6.269
Total thickness of cyst plates	11.111	----
Thickness of lower layer of cyst plates	9.943	6.236
Ratio of lower layer to total thickness	1.756	3.54

Table 1: Coefficients of variation of three latilaminae in specimens A50/B/1 and A50/B/2

	LAT. 4	LAT. 5
Width of broad cyst plates	3.108	4.634
Radius of broad cyst plates	16.32	6.127
Radius of arcuate cyst plates	10.66	8.76
Number of cyst plates per 4 mm:		
1) broad	12.834	8.57
2) arcuate	0.000	47.14
3) total	7.971	16.835
Number of pillars per 4 mm.	4.929	6.149
Thickness of the pillars	9.038	8.94
Total thickness of cyst plates	0.01	0.000
Thickness of lower layer of cyst plates	0.01	10.86
Ratio of lower layer to total thickness	2.916	0.585

Table 2: Coefficients of variation in three sections of two latilaminae in one individual. Calculated for two latilaminae in A50/B/1.

different ages are involved.

The coefficients of variation calculated here are extreme and inconsistant. The parameters having near average values are the width of the broad cyst plates, the radius of the broad cyst plates and the number of pillars per 4 mm.

The method is very simple and rather crude and may be valid in zoological studies, where there is strict control over the population. In palaeontological studies, where the control over the population is limited, the formula is of little value and was not used further in this study.

Student's 't'

Student's 't' test provides a method of determining the probability that the difference between the mean values of a parameter, of two samples, could have arisen by chance. Student's 't' is roughly the difference between the two sample means, divided by a measure of the standard deviation of that difference. The value of 't', when located in the table of 't' against the corresponding number of degrees of freedom, gives the probability that the difference between the two means is purely by chance. For the purpose of this study, the probabilities have been converted to a percentage probability that the two means are the same.

The formula used was:

$$t = \frac{(\bar{X}_1 - \bar{X}_2)\sqrt{\frac{N_1 N_2}{N_1 + N_2}}}{\sqrt{\frac{(N_1 - 1)S_1^2 + (N_2 - 1)S_2^2}{N_1 + N_2 - 2}}}$$

where: $\bar{X}_1$ - the mean of the variate 1,

$\bar{X}_2$ - the mean of the variate 2,

N_1 - the number of measurements of variate 1,

N_2 - the number of measurements of variate 2,

S_1 - the standard deviation of variate 1,

S_2 - the standard deviation of variate 2.

The Student's 't' tests were carried out on the McGill University I.B.M. computer 7040/44. The programme is included in the back pocket.

These tests were applied to make comparisons between:

1) the mean values of parameters in three latilaminae in one individual,

2) the mean values of parameters in three individuals from one sample station.

The results are given in tables 3 and 4 respectively.

Table 3 shows that for most parameters the probability that the samples were drawn from the same population is very small. The probabilities show that, on the basis of Student's 't', the difference between two latilaminae of one individual is real and not due to chance. This is very significant as it shows that the measurements from one latilamina are not characteristic of the individual. Further, that the definition of a species by measurements taken from one latilamina is invalid.

The probabilities, for the total thickness of the cyst plates, the thickness of the lower layer and the ratio of these two measurements, are extremely variable in table 3. This indicates that the mean values of these parameters are inconsistant within an individual and supports the earlier contention that the layering in the cyst plates is of secondary origin and has no taxonomic significance.

The results of the comparisons between three individuals (the measurements of several latilaminae in one individual

	% PROBABIDITIES		
LATILAMINAE	4:5	4:6	5:6
Width of broad cyst plates	16	74	81
Radius of broad cyst plates	14	52	36
Number of cyst plates per 4 mm:			
1) broad	71	97	83
2) arcuate	99.9	99.9	55
3) total	98	55	74
Number of pillars per 4 mm	15	16	30
Thickness of the pillars	26	62	43
Total thickness of cyst plates	71	10	62
Thickness of lower layer of cyst plates	85	44	57
Ratio of lower layer to total thickness	81	76	10

Table 3: Results of Student's 't' tests between three latilaminae of one individual. Calculated for A50/B/1.

	% PROBABILITIES		
INDIVIDUALS	1:2	1:3	2:3
Width of broad cyst plates	96	98.7	60
Radius of broad cyst plates	50	10	50
Number of cyst plates per 4 mm:			
1) broad	89	99.9	70
2) arcuate	90	29	85
3) total	99.9	99.1	81
Number of pillars per 4 mm.	70	95	99
Length of the pillars	99.9	75	99.9
Thickness of the pillars	99.5	80	90
Total thickness of cyst plates	12	70	80
Thickness of lower layer of cyst plates	10	80	82
Ratio of lower layer to total thickness	24	88	70

Table 4: Results of Student's 't' tests between three individuals from one sample station. Calculated between A43/1,2 and 3.

combined) from one sample station (table 4) indicate that, on the basis of Student's 't' tests, certain parameters show that there is no real difference between the members of the group.

The 95% probability for two comparisons was used as a purely arbitrary and flexible lower limit in selecting parameters characteristic of the group; these are:

1) the width of the broad cyst plates,
2) the total number of cyst plates per 4 mm.,
3) the number of pillars per 4 mm.,
4) the length of the pillars.

The reason for the higher probabilities in table 4 compared to table 3 is that a greater sample is used. Even in the parameters most characteristic of the group, two probabilities are greater than 95% and one is less than 95% (eg. the length of the pillars). This could indicate that the two individuals having a low probability form the extreme members of the group. On the other hand, the low probability could be due to chance, indicating that the sample (three specimens from one station) was not large enough for the mean of any parameter to be truly representative of the group. Therefore, a larger sample is required to define the characteristics of a group. Further, to define a species, neither a single latilamina, nor three specimens, but many more individuals are required.

The use of multiple 't' tests is valid only when a small number of tests are involved. That is, it is invalid to compare A:B, A:C, B:C, A:D, B:D, C:D.....etc. indefinitely. It is, however, considered valid when only three individuals are compared, as in this study.

TAXONOMIC VARIATIONS

Mean Values

The mean values, for each parameter in each individual, are plotted as frquency distributions (figs. 6, 7, 8 and 9). The range and modal value of the population and the mean value of the holotype are given for each parameter in table 5.

The mean value of the holotype falls close to the modal value, only for the number of cyst plates per 4 mm. (fig. 7). Therefore, only in this one case, is the holotype representative of the population.

Standard Deviations

The standard deviations are plotted (fig. 10) in the same way as the mean values (see above). The range and modal value of the population, and the standard deviation of the holotype are given for each parameter in table 6.

In the holotype, the standard deviations of all the four parameters, except the width of the broad cyst plates, lie within the central distribution of the population (fig. 10). These standard deviations, as a measure of the variability within the individuals, indicate that, for all parameters except the width of the broad cyst plates, the holotype is representative of the population, with regard to the amount of variability within an individual.

't' Tests

The holotype was compared with each individual, using the Student's 't' test. The results are plotted as

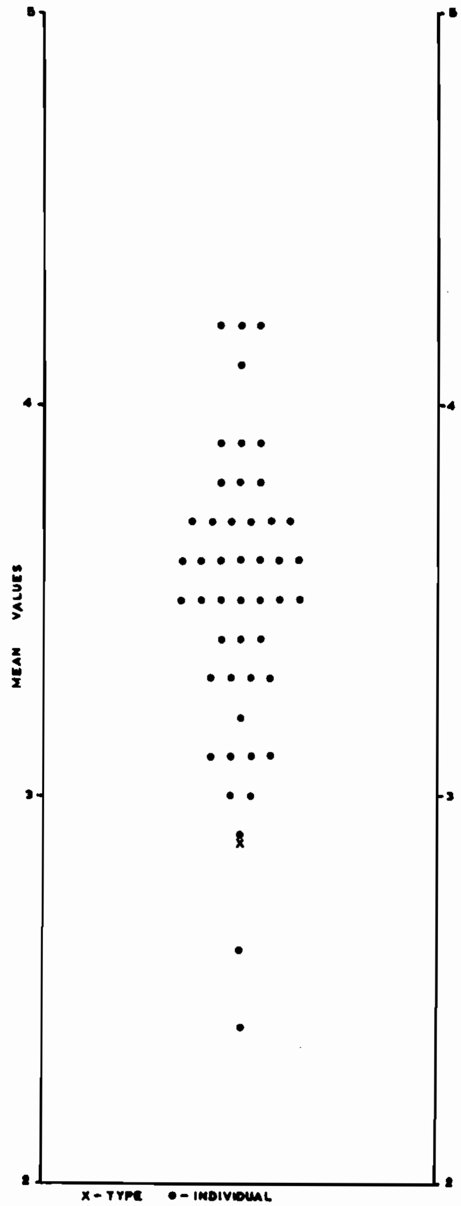


Fig. 6: Frequency distribution of the mean values of the width of the broad cyst plates.

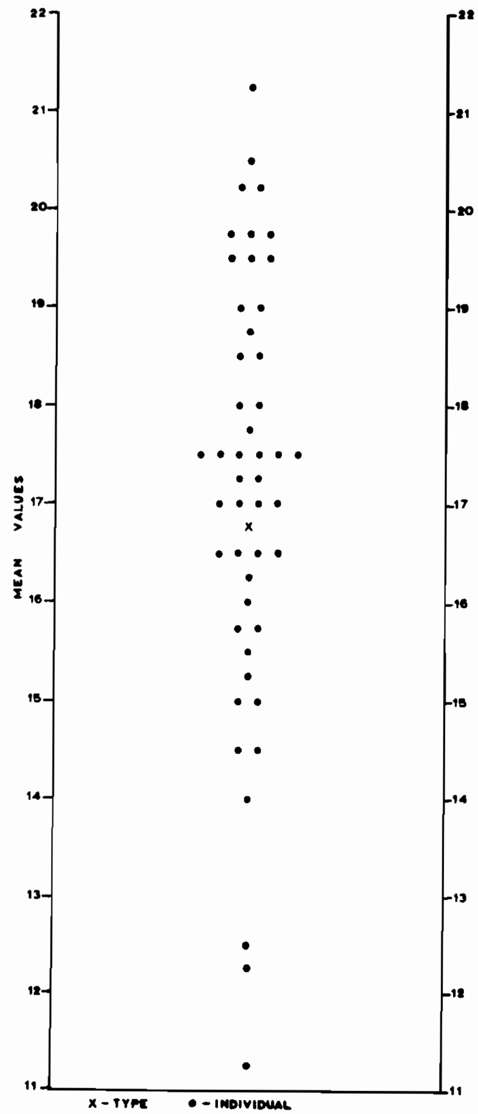


Fig. 7: Frequency distribution of the mean values of the total number of cyst plates per 4 mm.

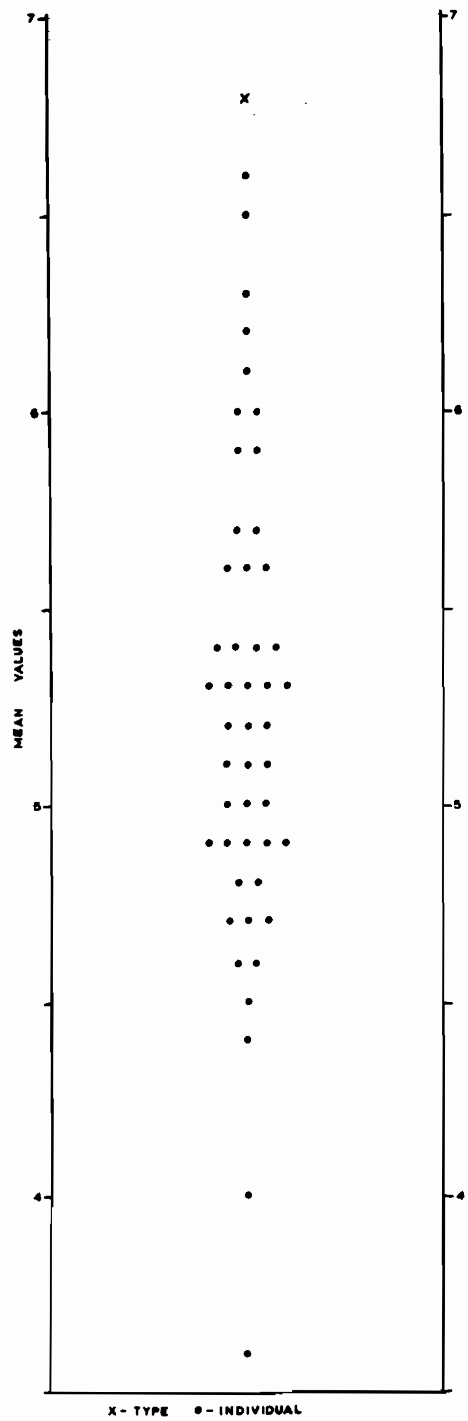


Fig. 8: Frequency distribution of the mean values of the number of pillars per 4 mm.

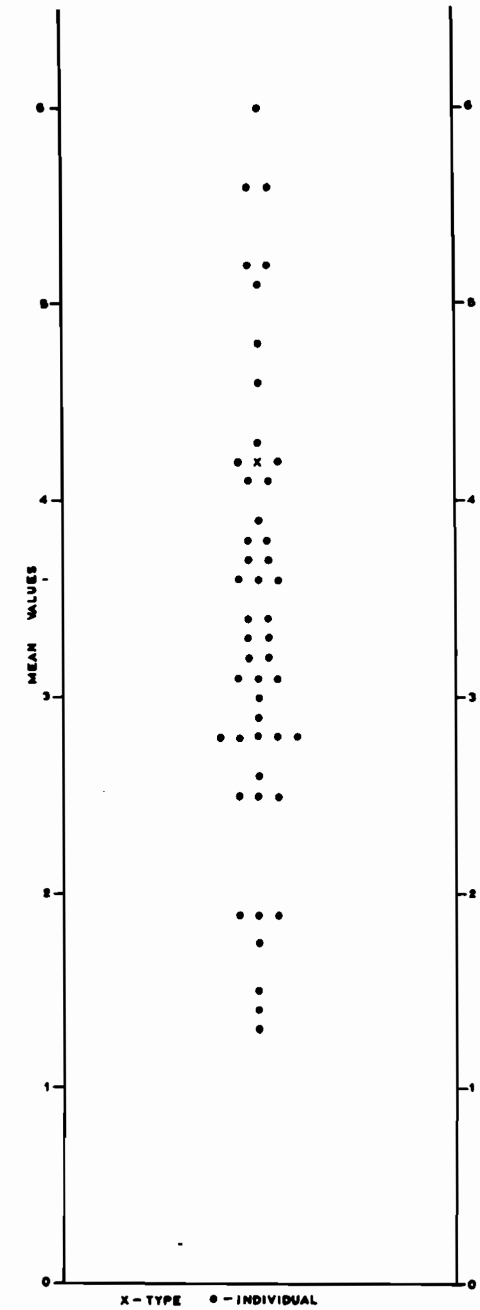


Fig. 9: Frequency distribution of the mean values of the length of the pillars.

PARAMETER	RANGE	MODE	TYPE
Width of broad cysts	2.4 - 4.2	3.6	2.7
No. of cysts per 4 mm.	11.2 - 21.2	17.5	16.75
No. of pillars per 4 mm.	1.3 - 6.0	2.8	4.2
Length of the pillars	3.6 - 6.6	5.3/4.9	6.8

Table 5: Mean values of individuals.

PARAMETER	RANGE	MODE	TYPE
Width of broad cysts	0.45 - 1.15	0.75	1.1
No. of cysts per 4 mm.	0.85 - 3.6	1.6	1.3
No. of pillars per 4 mm.	0.5 - 1.6	0.8/1.15	0.9
Length of the pillars	0.25 - 2.15	1.0	0.97

Table 6: Standard deviations of individuals.

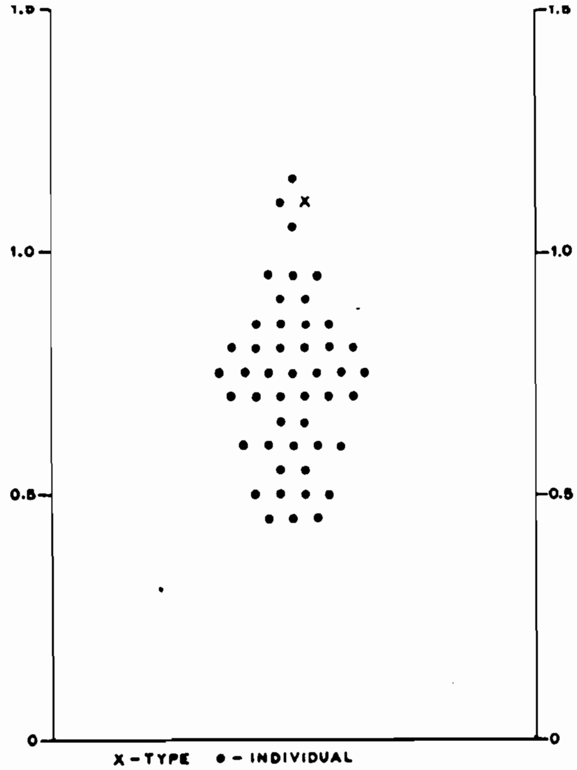
Fig. 10: Frequency distribution of the standard deviations of the parameters:

A) width of the broad cyst plates,

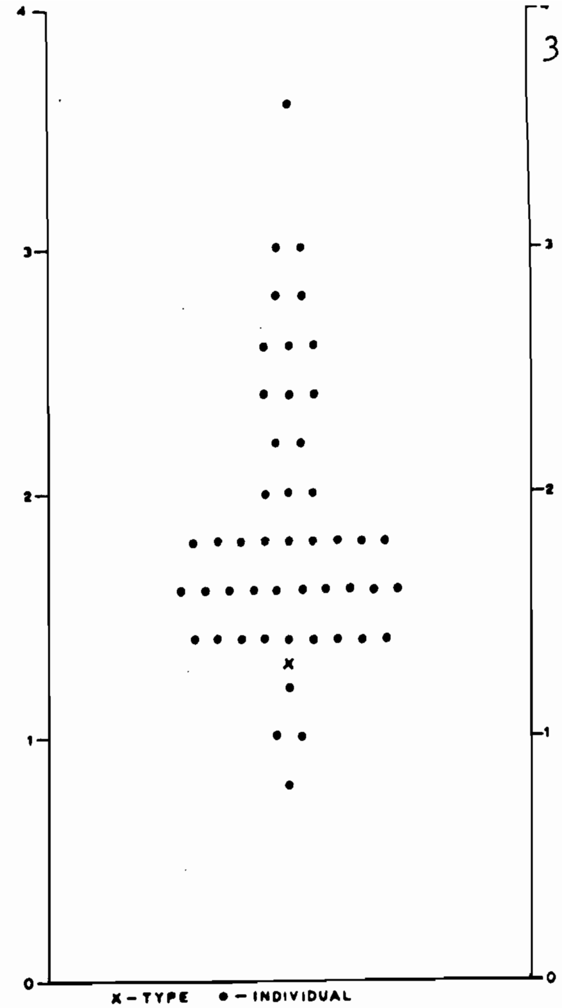
B) total number of cyst plates per 4 mm.,

C) number of pillars per 4 mm.,

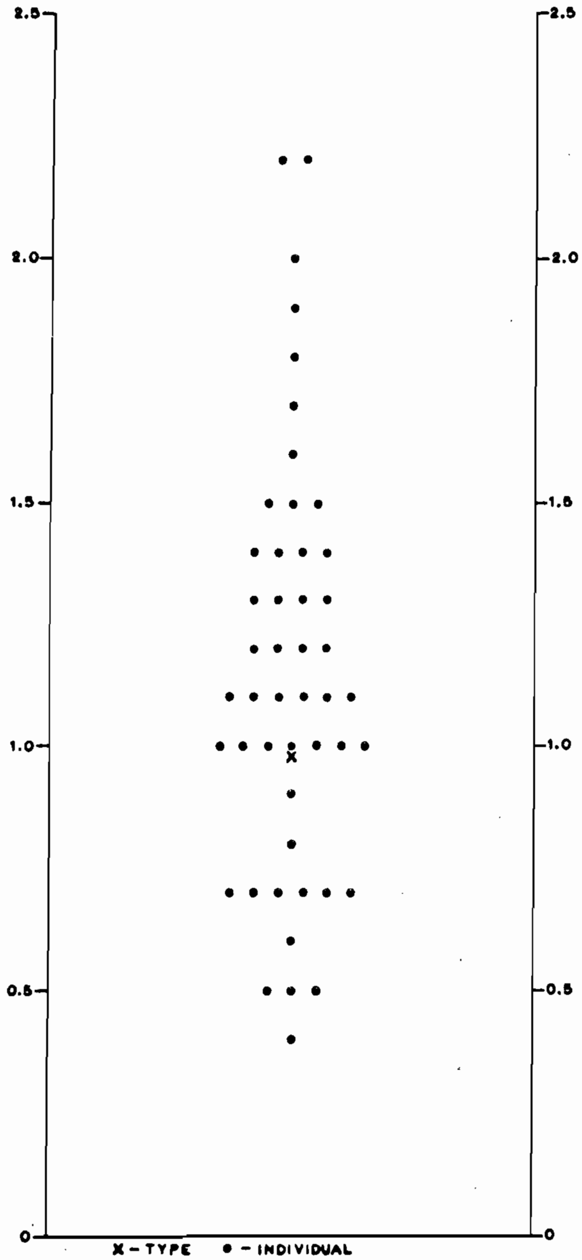
D) length of the pillars.


X-TYPE • - INDIVIDUAL

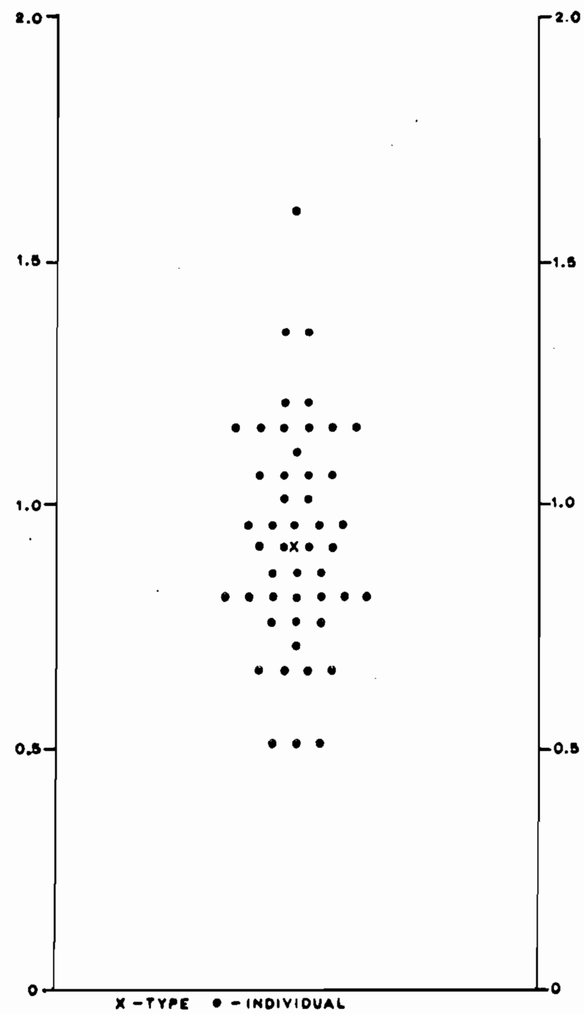
A.


X-TYPE • - INDIVIDUAL

B.


X-TYPE • - INDIVIDUAL

D


X-TYPE • - INDIVIDUAL

C

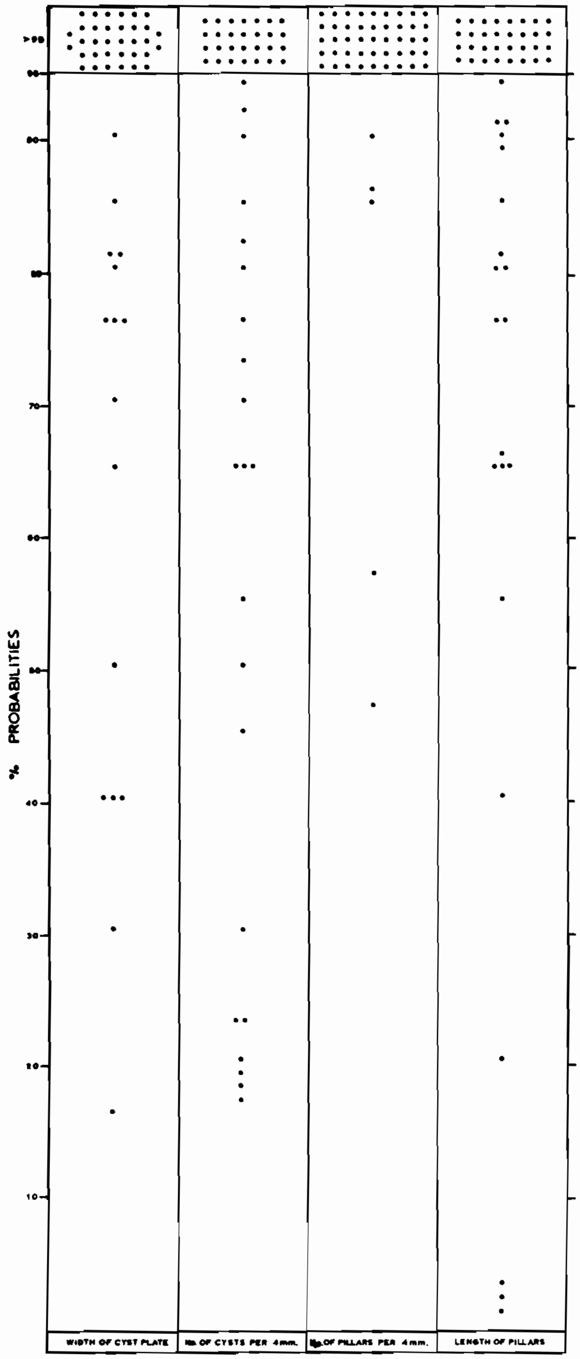


Fig. 11: Probabilities that individuals are the same as the holotype.

percentage probabilities for the four parameters (fig. 11)

For each parameter, most points lie above the level of 95% probability that the individual is the same as the type. Some points will fall above or below the 95% level by chance. There is, however, only one concentration of points. If two species are present, the probabilities would fall into two concentrations. Therefore, it is suggested that all the individuals are of the same species.

To test for any real difference between the individuals with greater than 95% probability and those with less than 95% probability, 't' tests were carried out between these two groups. For each parameter, the probability that the groups are the same is greater than 99.9%. This substantiates the contention that the individuals are of the same species.

Conclusions

From the above observations, the following conclusions can be drawn:

1) on the basis of the mean values of the parameters, the holotype is generally atypical of the population,

2) on the basis of the variability within an individual, the holotype is representative of the population,

3) all the individuals are of the same species, which includes the holotype.

GEOGRAPHIC VARIATIONS

With the four parameters selected above, tests were made to determine if the mean value of any parameter varies systematically across the area; that is if there is any correlation between mean values and geographic distribution.

Method

Initially, the mean values for each parameter, at each sample station, were plotted geographically (figs. 12, 14, 16 and 18). From these plots, possible trend directions were established, by eye and by trial plots. The mean values were projected perpendicularly on to the line of maximum trend and then plotted on a graph against the distance along the direction of maximum trend, (figs. 13, 15, 17 and 19, which correspond to figs. 12, 14, 16 and 18 respectively). Trend lines were fitted to the scatter of points by the method of least squares.

The following tests were carried out on the trend lines:

1) does the slope of the line (b_{yx}) differ significantly from zero, i.e. is there any regression? This is calculated by means of the correlation coefficient (r_{yx}), which is a measure of the closeness of fit of the line. The value of r_{yx} can vary from 1 to -1. A value of unity means there is perfect fit, a value of infinity, no fit at all. When r_{yx} is positive the line slopes upward from left to right (positive regression), when negative, it slopes upward from right to left (negative regression).

The formula is:

$$r_{yx} = \frac{\frac{\Sigma(x-\bar{x})(y-\bar{y})}{N}}{S_x . S_y}$$

where: S - the standard deviation,

x - the horizontal distance,

y - the mean value,

N - the number of mean values.

From this, the standard error of estimate (SEE) of the slope of the line (b_{yx}) is calculated:

$$SEE_{b_{yx}} = S\sqrt{1 - r_{yx}^2}$$

which allows the calculation of the standard error of the slope of the line $(SE_{b_{yx}})$:

$$SE_{b_{yx}} = \frac{SEE_{b_{yx}}}{\sqrt{\Sigma(x-\bar{x})^2}}$$

the probability of any regression is then calculated:

$$t = \frac{b_{yx}}{SE_{b_{yx}}}$$

The value of 't' is located in the table of 't' and the corresponding probability recorded as a percentage probability that there is regression.

2) does the correlation coefficient (r_{yx}) differ significantly from zero, i.e. is there any correlation between the mean values and geographic distance? This is calculated by the formula:

$$t = \sqrt{\frac{N-2}{(1 - r_{yx}^2)}}$$

The value of 't' is located as above and the probability that there is any correlation is recorded as a percentage value.

<u>Results</u>

The statistical values for correlation and regression are given in table 7.

<u>Width of the broad cyst plates</u>: The geographical and graphical plots show a very slight decrease in the mean values from west to east. There is, however, only a 67% probability of regression and only a 44% probability of correlation. It is concluded that the width of the broad cyst plates does not

Fig. 12: Geographical plot of mean values.

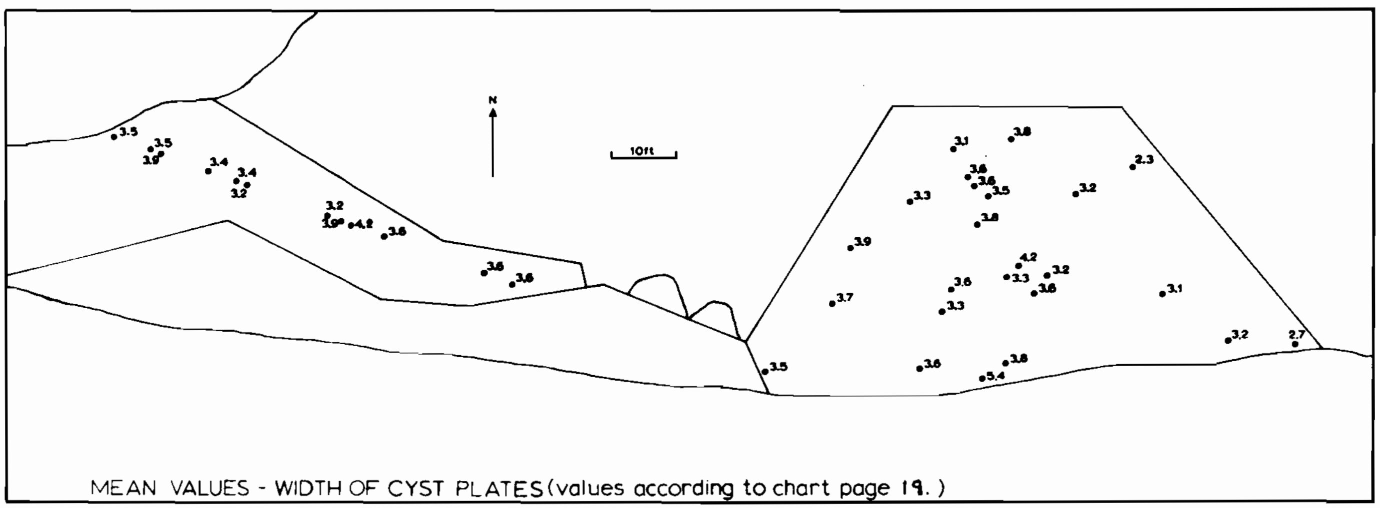


Fig. 13: Regression line for the width of the broad cyst plates.

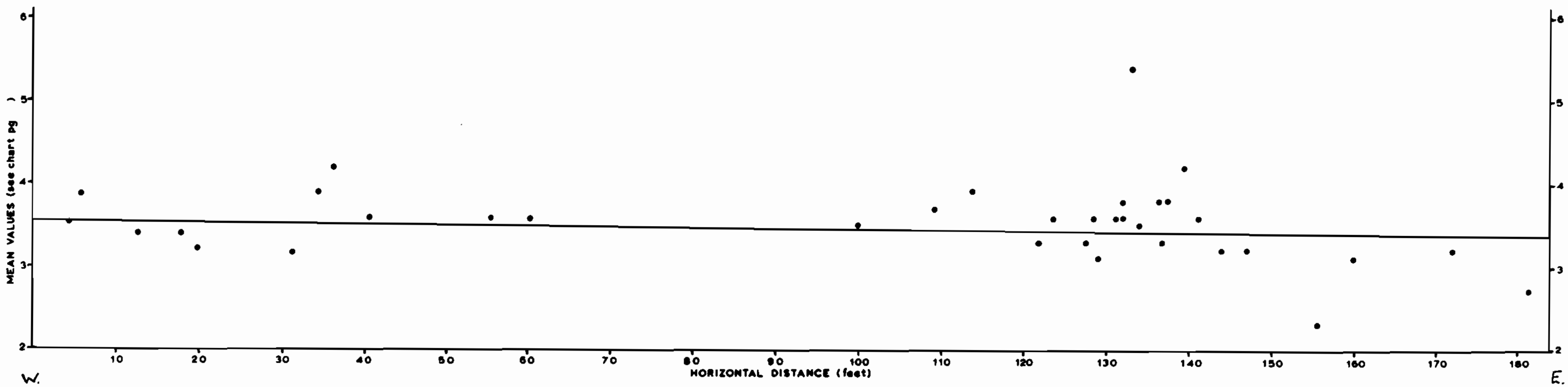


Fig. 14: Geographical plot of mean values.

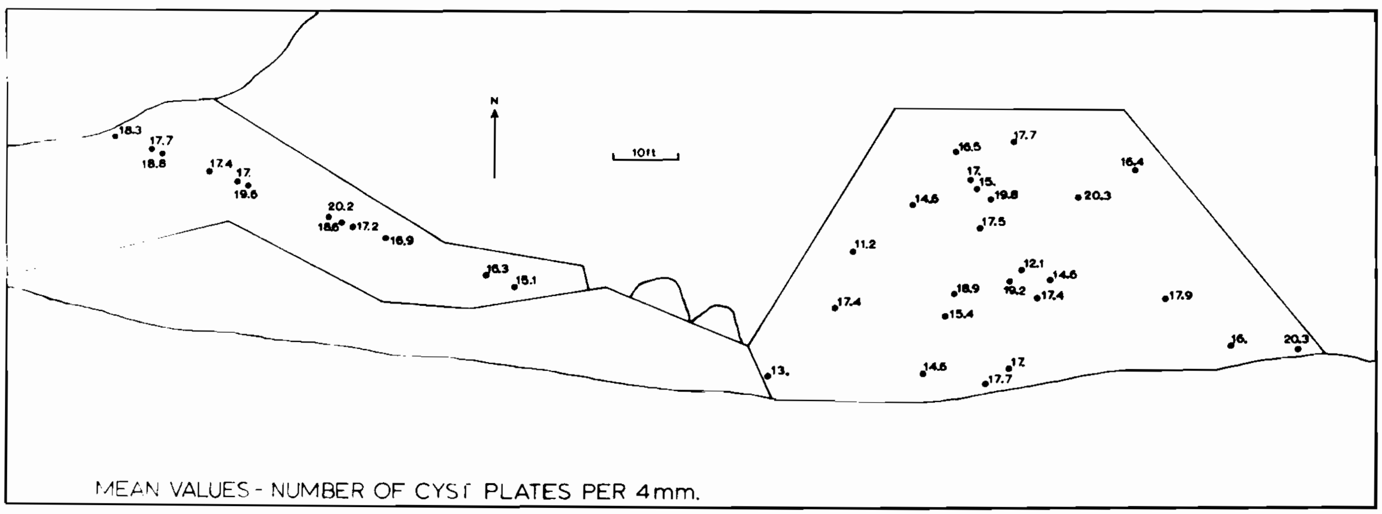


Fig. 15: Regression line for the total number of cyst plates per 4 mm.

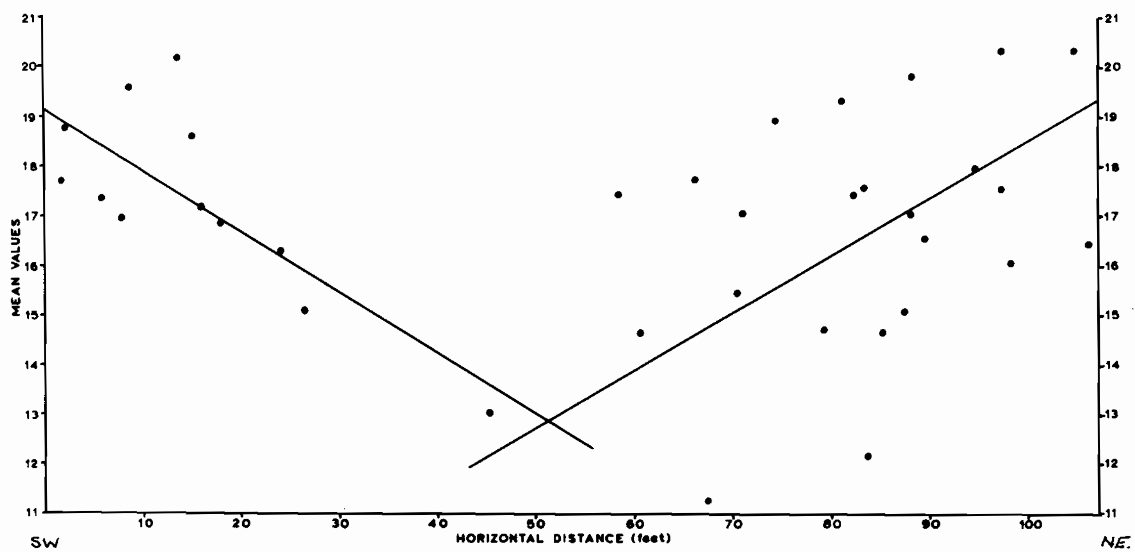


Fig. 16: Geographical plot of mean values.

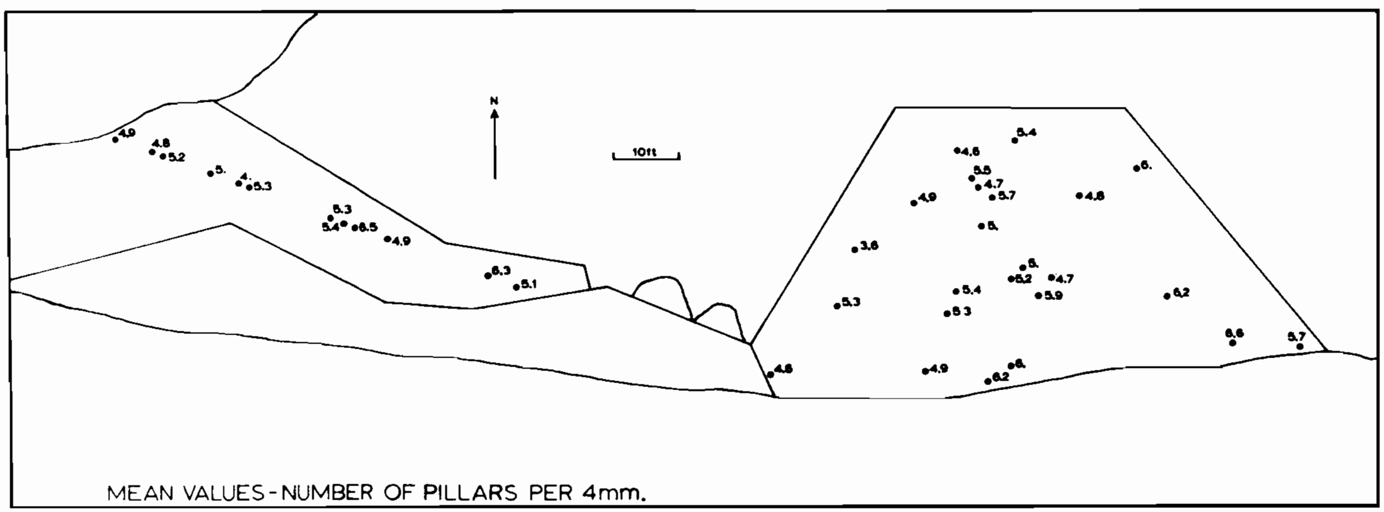


Fig. 17: Regression line for the number of pillars per 4 mm.

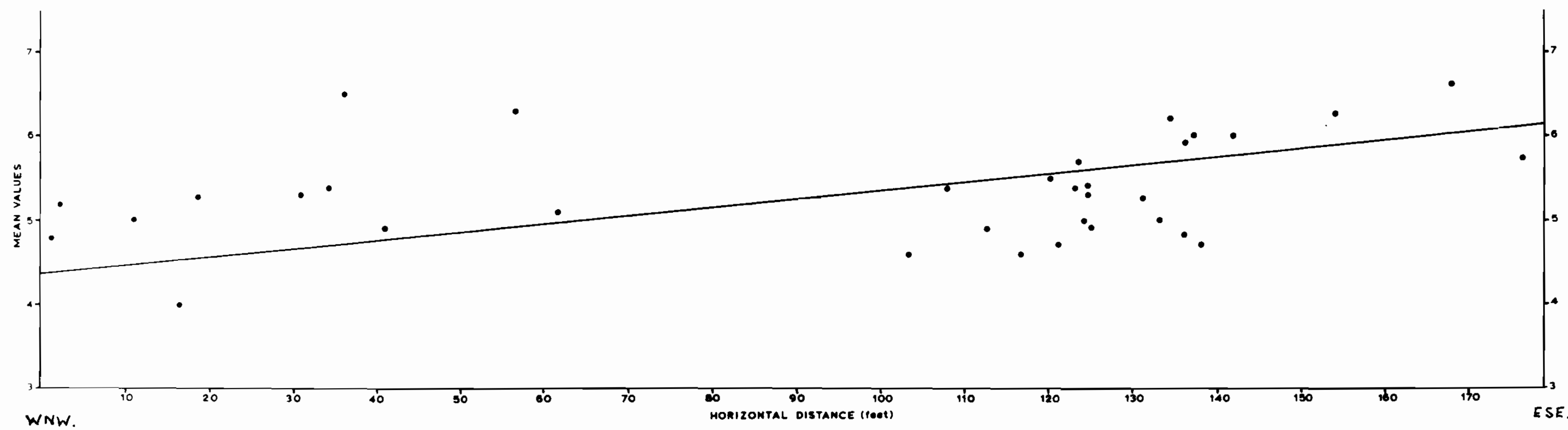


Fig. 18: Geographical plot of mean values.

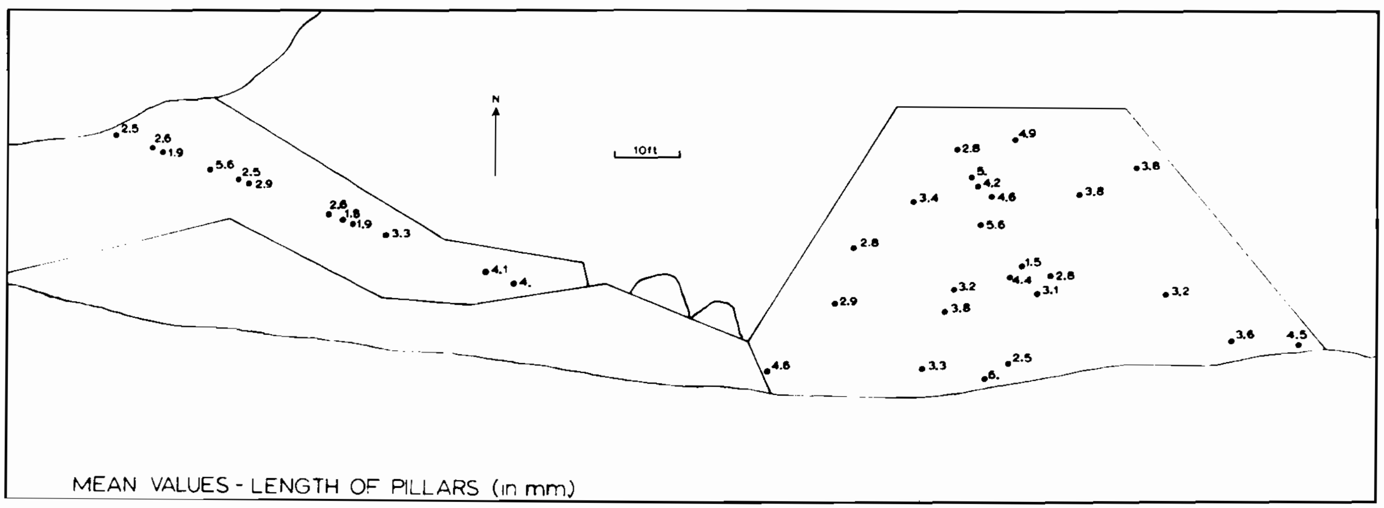
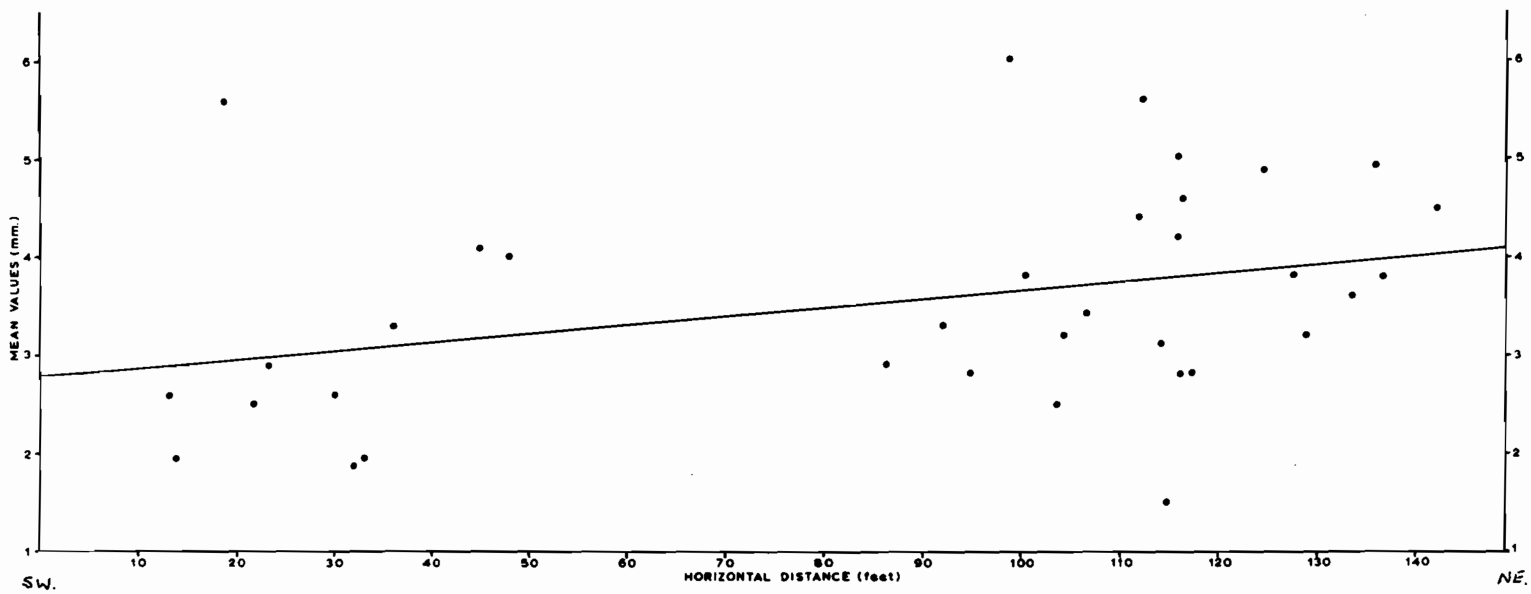


Fig. 19: Regression line for the length of the pillars.



PARAMETER		Slope of the line b_{yx}	Standard error of estimate $SEE_{b_{yx}}$	Standard error $SE_{b_{yx}}$	Does b_{yx} differ significantly from zero?	Correlation coefficient r_{yx}	Does r_{yx} differ significantly from zero?
Number of cysts per 4 mm.	E.	1·147	4·87	0·666	91%	0·137	49%
	W.	−1·22	1·166	0·283	99·8%	−0·785	99·5%
Width of broad cyst plates		−0·01421	0·485	0·016	67%	−0·095	44%
Number of pillars per 4 mm		0·095	0·471	0·0156	>99·9%	0·697	>99·9%
Length of the pillars.		0·03515	1·058	0·043	>99·9%	0·303	93%

Table 7: Statistical values for correlation and regression.

vary systematically with geographic distance.

Total number of cyst plates per 4 mm: In the southwestern section there is a marked decrease in the mean values towards the northeast, with a 99.8% probability of regression and a 99.5% probability of correlation. In the northeastern section there is a 91% probability of regression, but only a 49% probability of correlation. This low value is due to the wide scatter of points about the line. From the graphical plot (fig. 15) and the high probability of regression, it is apparent that the mean values vary systematically with geographic distance, but the wide scatter of points about the line conceals this in the statistical results.

Number of pillars per 4 mm: The established trend for this parameter is an increase in mean values towards the east-southeast. There is a greater than 99.9% probability of regression and a greater than 99.9% probability of correlation and therefore, a very close correlation between mean values and geographic distance.

Length of the pillars: There is an increase in the mean values towards the northeast. The probability of regression is greater than 99.9% and the probability of correlation is 93%. Therefore, the mean values of this parameter also, vary systematically with distance.

Summary

The mean values of the total number of cyst plates per 4 mm., the number of pillars per 4 mm. and the length of the pillars have a linear correlation with distance. This could be of palaeogeographic significance.

The variations in mean values cannot be related to palaeoenvironment in this study, because the area is limited in size and no evidence of palaeoenvironmental change was found. The possible current directions are:

1) from the NNE.,
2) from the ESE.,
3) from the WNW.

and the parameters show:

1) a decrease and increase to the nertheast (number of cyst plates per 4 mm.),
2) an increase to the east-southeast (number of pillars per 4 mm.),
3) an increase to the northeast (length of the pillars).

If the current direction affects the mean values, then:

1) the length of the pillars increases in an upcurrent direction,
2) the number of pillars increases or decreases in an upcurrent direction.

The linear correlation between mean values and geographic distance supports the contention that the stromatoporoids grew where they now lie, or within a short distance of it. If the stromatoporoids were washed into the area and randomly distributed, the probability of correlation between mean values and geographic distance would be very low. This proceedure, therefore, distinguishes between an indigenous and an introduced community and may be applicable to other taxa.

CONCLUSIONS

Previous work on the palaeoecology of stromatoporoids has been based on the gross morphology of the coenosteum. Massive stromatoporoids indicate shallow water, turbulent environments. The massive stromatoporoids of the Ouareau river grew in a quiet, shallow water, carbonate shelf environment, in which lime muds were deposited and subsequently pelleted.

The prevailing current direction, indicated by orthoceraconic cephalopods, was from:

1) the east-southeast,

or 2) the west-northwest,

or 3) the north-northeast.

The cyst plates are tripartite. The median layer of the cyst plates is narrow and dense, the upper layer is wider and less dense and the lower layer, generally the widest, is of similar appearance as the upper layer. Only in parts of a few individuals are the layers of the cyst plates like those of the holotype.

The pillars are composed of dense material, when well preserved. Generally, they consist of a median zone of granular calcite and a narrow, outer zone of dense material. Where the pillars are dense, the cyst plates are often continuous across the pillars.

The less dense, granular layers of the cyst plates and pillars are considered to be of secondary origin.

The use of the coefficient of variation is invalid in palaeontological studies, because of the lack of homogeneity in the population sampled.

Student's 't' tests indicate that measurements from one latilamina are not representative of the individual and the definition of a species by these measurements would be invalid. The tests indicate that measurements of the width of the broad cyst plates, the number of cyst plates per 4 mm., the number of pillars per 4 mm. and the length of the pillars are representative of a group of individuals from the same sample station. Even here, the parameters are not entirely representative. The definition of the species should therefore be based on a larger collection.

The mean values of the following parameters are correlated with geographic distance across the bed:

1) the number of cyst plates per 4 mm.,
2) the number of pillars per 4 mm.,
3) the length of the pillars.

This correlation may be related to current direction and shows the population to be indigenous and not introduced.

The mean values of parameters in the holotype are generally atypical of the population, but the amount of variability within the holotype is generally typical of the population.

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PLATE ONE

Fig. 1: Surface of the bed, showing the density of the stromatoporoids.

Fig. 2: Typical section, showing types of cyst plates and dense pillars (x 15, approx.).

Fig. 3: Tripartite form of the cyst plates (x 70, approx.).

Fig. 1.

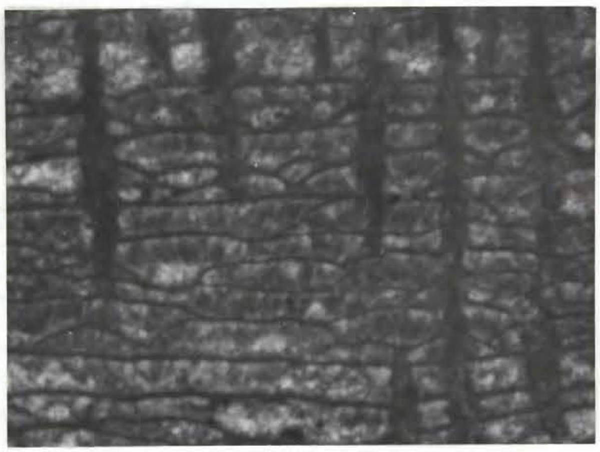

Fig. 2.

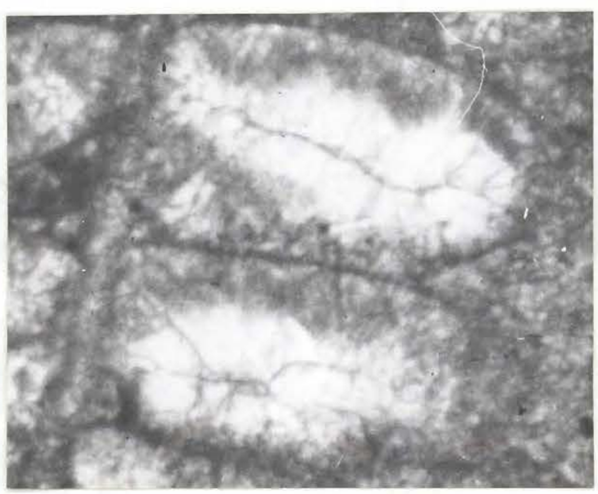

Fig. 3.

PLATE ONE

PLATE TWO

Fig. 1: Composition of the pillars. Median layer of the cyst plates continuous with the outer layer of the pillars. Some cyst plates similar to those of the holotype (x35, approx.).

Fig. 2: Dense pillars with cyst plates continuous across the pillars (x30, approx.).

Fig. 1.

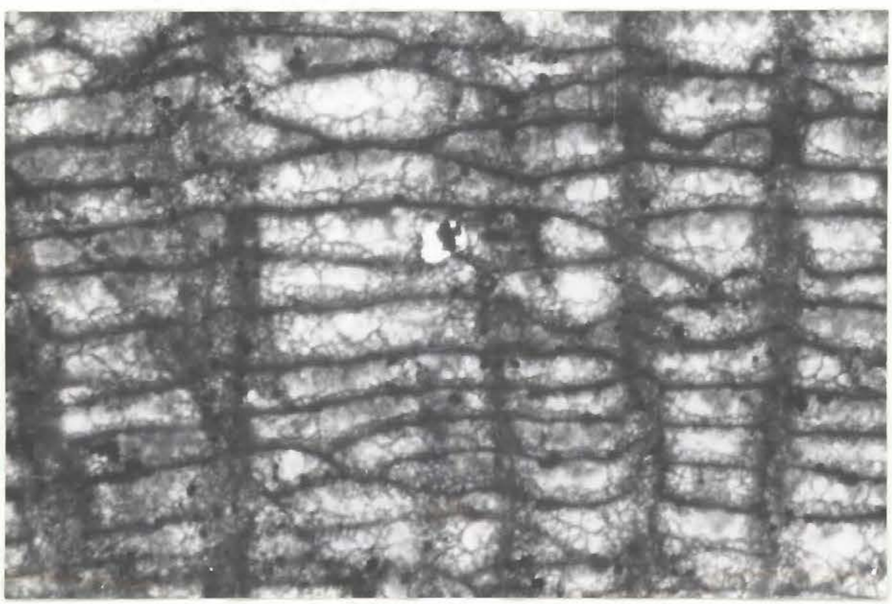

Fig. 2.

PLATE TWO

```
 ISN      SOURCE STATEMENT

   0 $IBFTC MAIN
   1          DIMENSION X(20),S(12),N(99),FMT(13),S1(12),S2(12),SUM(12),SUM2(12)
             1,XM(12),XM1(12),XM2(12),M(10),M1(10),M2(10)
   2        1 READ(5,2)L,LL,LS
   6        2 FORMAT(16I5)
   7          READ(5,2)(N(I),I=1,LL)
  14          READ(5,3)FMT
  15        3 FORMAT(13A6)
  16          WRITE(6,200)
  17          DO 10 I=1,LL
  20          NN=N(I)
  21          DO 5 J=1,12
  22          SUM(J)=0.
  23        5 SUM2(J)=0.
  25          DO 50 J=1,L
  26       50 M(J)=N(I)
  30          DO 9 J=1,NN
  31          READ(5,FMT)(X(II),II=1,L)
  36          DO 9 II=1,L
  37          IF(X(II).EQ.0.)M(II)=M(II)-1
  42          SUM(II)=SUM(II)+X(II)
  43        9 SUM2(II)=SUM2(II)+X(II)**2
  46          DO 8 II=1,L
  47          XM(II)=SUM(II)/FLOAT(M(II))
  50        8 S(II)=SQRT((SUM2(II)-SUM(II)**2/FLOAT(M(II)))/FLOAT(M(II)-1))
  52          IF(I.NE.1)GO TO 7
  55          DO 6 II=1,L
  56          XM1(II)=XM(II)
  57          M1(II)=M(II)
  60        6 S1(II)=S(II)
  62          GO TO 10
  63        7 IF(I.EQ.2.AND.LS.EQ.1)GO TO 11
  66          IF(LS.EQ.1)GO TO 15
  71          DO 12 II=1,L
  72          T=(XM1(II)-XM(II))*SQRT(FLOAT(M1(II)*M(II))/FLOAT(M1(II)+M(II)))/S
             1QRT((FLOAT(M1(II)-1)*S1(II)**2+FLOAT(M(II)-1)*S(II)**2)/
             2FLOAT(M1(II)+M(II)-2))
  73       12 WRITE(6,20)II,M1(II),M(II),XM1(II),XM(II),S1(II),S(II),T
  75       20 FORMAT(1HJ,12X,3I5,5F14.7)
  76          GO TO 10
  77       11 DO 13 II=1,L
 100          XM2(II)=XM(II)
 101          M2(II)=M(II)
 102       13 S2(II)=S(II)
 104       10 CONTINUE
 106          STOP
 107       15 WRITE(6,201)
 110          DO 25 II=1,L
 111          T=(XM1(II)-XM2(II))*SQRT(FLOAT(M1(II)*M2(II))/FLOAT(M1(II)+M2(II))
             1)/SQRT((FLOAT(M1(II)-1)*S1(II)**2+FLOAT(M2(II)-1)*S2(II)**2)/FLOAT
             2(M1(II)+M2(II)-2))
 112       25 WRITE(6,20)II, M1(II),M2(II),XM1(II),XM2(II),S1(II),S2(II),T
 114          WRITE(6,202)
 115          DO 26 II=1,L
 116          T=(XM1(II)-XM(II))*SQRT(FLOAT(M1(II)*M(II))/FLOAT(M1(II)+M(II)))/
```



```
 ISN      SOURCE STATEMENT

             2SQRT((FLOAT(M1(II)-1)*S1(II)**2+FLOAT(M(II)-1)*S(II)**2)/FLOAT(M1(
             2II)+M(II)-2))
 117       26 WRITE(6,20)II,M1(II),M(II),XM1(II),XM(II),S1(II),S(II),T
 121          WRITE(6,203)
 122          DO 27 II=1,L
 123          T=(XM2(II)-XM(II))*SQRT(FLOAT(M2(II)*M(II))/FLOAT(M2(II)+M(II)))/
             2SQRT((FLOAT(M2(II)-1)*S2(II)**2+FLOAT(M(II)-1)*S(II)**2)/FLOAT(M2
             3(II)+M(II)-2))
 124       27 WRITE(6,20)II,M2(II),M(II),XM2(II),XM(II),S2(II),S(II),T
 126      200 FORMAT(1H1,28X,12HMEAN GROUP 1,2X,12HMEAN GROUP 2,2X,12HS.D. GROUP
             1 1,2X,12HS.D. GROUP 2,6X,6HT-TEST)
 127      201 FORMAT(1HK,13HGROUP 1 AND 2)
 130      202 FORMAT(1HK,13HGROUP 1 AND 3)
 131      203 FORMAT(1HK,13HGROUP 2 AND 3)
 132          STOP
 133          END
```