BRACHIOPOD COMMUNITIES IN AVONIAN REEF LIMESTONES OF THE PENNINES

By

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C O N T E N T S

I. INTRODUCTION.

The importance of variation study in systematics and in evolutionary series is receiving ever widening recognition. In stratigraphy such studies have already proved their use in distinguishing between successive horizons notably in the Coal Measures.

Among stratigraphical deposits where such a study may prove of value, are the reef limestones of Northern England (fig.1). These have provided many stimulating problems, not the least of which is the determination of their age. Detailed mapping on conventional stratigraphical lines has been the main method of approach to this problem in the past, and only recently have the species-assemblages, locally so abundant, been used in their entirety to assist the determination of the stratigraphical level of these limestones.

The present work is intended as a further contribution to this end. The material for study has been provided by localised collecting of brachiopod assemblages from the reef limestones of Craven and North Derbyshire. From the random samples, specimens of Schizophoria resupinata and Martinia aff.glabra have been extracted, and it is on these unitary demes that the analysis is based. Conventional statistical techniques have been employed including methods of multivariate analysis. The statistical differences demonstrated are interpreted by the following considerations. Variation may be due to differences in genetic constitution of the populations, it may be attributable to the modifying effects of environment, or it may arise if the samples studied are derived from populations of different ages.

Some of the variation is shown to be genetic and may be due to differences at a specific or sub-specific level. Some is best considered as due to the impress of environment. The variation which remains is insignificant and accordingly the deposits which have yielded the samples are considered contemporaneous.

ACKNOWLEDGEMENTS.

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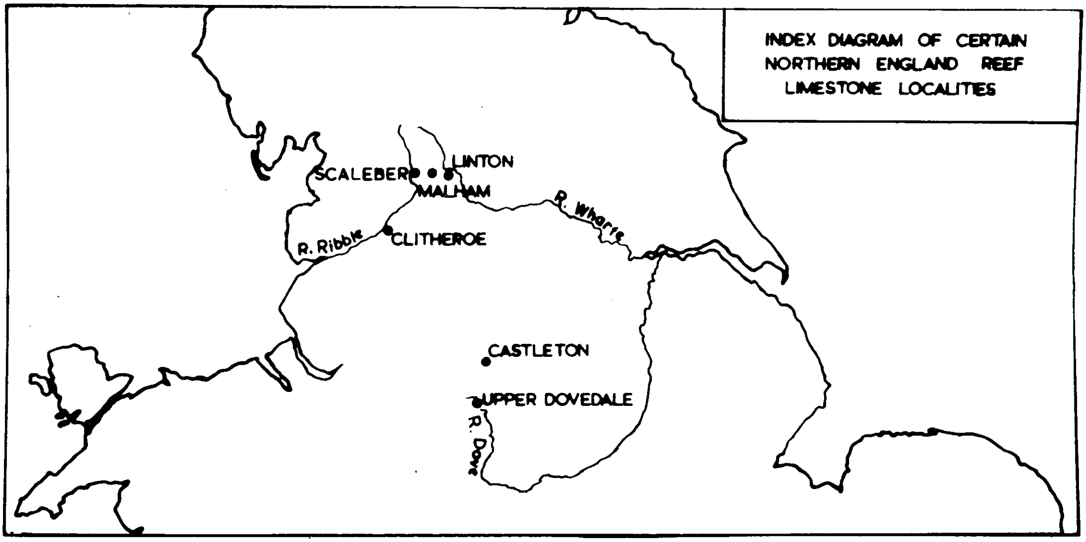


Fig.1.- Principal areas of Avonian reef-limestones in the Pennines.

II. HISTORY OF PREVIOUS RESEARCH.

Variation studies in which the emphasis is stratigraphical or ecological rather than purely taxonomic are becoming increasingly important in palaeontological literature.

In a beautifully illustrated account, based on the measurement of 2000 specimens, Rowe (1899) was able to demonstrate zonal variation in the echinoid genus Micraster. Carruthers (1910) gave a well-founded analysis of the ontogenetic and evolutionary changes in morphology of Zaphrentis delanouei in the Lower Carboniferous. The use of progressively incurved specimens of Gryphaea in the correlation of the Lower Lias has been described by Trueman (1922).

In recent years there has been an increase in variation studies of this sort. Elias (1937) illustrates how the gradual increase of distance between the branches, dissepiments, and zooecia of certain fenestrate bryozoans, can be correlated with successively later major stratigraphical subdivisions of the Carboniferous and Permian. Applying the ribbing formula he evolved (1928) for the Orthacea, Bancroft, in a paper published posthumously (1945), has been able to establish no fewer than 32 minor zones in the lower half of the Upper Ordovician of Britain. Wood and Barnard (1946), basing their results on inch by inch collecting over a small vertical distance in the Upper Lias of Northamptonshire, have shown a variation in the foraminiferal genus Opthalmidium.

Perhaps the best known variation studies of stratigraphical importance are those based on the changes in shell shape of certain non-marine lamellibranch genera of the family Anthracosiidae. On this variation is based the zonal scheme proposed for the South Wales coalfield (Davies and Trueman 1927) and since extended to the Ruhr and the Donetz. Recent variation studies in this field include those of Leitch (1940) MacLennan (1944) and Eagar (1946), while summaries of the variation and its zonal significance are given by Trueman (1946-47) Trueman and Weir (1946) and Leitch (1951).

An important recent work is that of Parkinson (1952 MS.) concerning the vertical and lateral variation in samples of Schizophoria resupinata at successive Lower Carboniferous horizons from C_2 to D_1.

Variation from a purely taxonomic viewpoint is discussed in the work of Bond (1941) in which a clearer definition of the species of Schizophoria is attempted.

Essentially quantitative studies on variation in communities of present day faunas, in geographically widely separated localities, have been made by Nicol (1944, see also Burma 1948) on the foraminiferan Elphidium, and Schenck (1945) on molluscan assemblages. Both lead to the possibility of interpreting the changes in conditions in Pliocene and Quaternary times.

In conclusion, some reference should be made to the ecological variation studies made on lamellibranch faunas.

The economically important genus Cardium has been the subject of repeated examination, and the control of different environmental factors has been noted. Walton (1919) commented on the difference in size and numbers of individuals on substrata of different texture. The effect of currents in relation to growth rate has been observed by Fraser (1931), while a decrease in the number of ribs has been correlated with a decrease in salinity in a paper by Purchon (1939). Eagar (1948) has noted that in the fresh-water Unionidae an increase in obesity occurs in slow moving or quiet conditions, while upstream, where the rate of water movement is higher, compressed forms occur. Variation in the degree of tolerance of muddy water in different species of fresh-water mussels is discussed. He includes a detailed summary of similar variation studies carried out in Britain, in Germany and in the United States.

III. METHOD OF STUDY.

The purpose of the present work is two-fold. Primarily an attempt is made to distinguish between communities of a single species of brachiopod. Secondly, the variation in form displayed by the population samples is illustrated and its taxonomic significance discussed.

Field Collecting.

Areas visited. The reef knoll limestones of the Craven area, particularly those near Cracoe (Bond 1950), have yielded the major part of the material examined. Collecting in this area has ranged from Hartlington Kail in the East to the knolls of Swinden and Elbolton in the West (fig.2). The Knoll limestones of Malham at Cawden Hill and Wedber Brow (Hudson 1930a) and those at Settle (Hudson 1930b) have also been visited. In Derbyshire, the bulk of the samples has been collected from Treak Cliff near Castleton (Shirley and Horsefield 1940, Parkinson 1947), and smaller quantities from localities on the arcuate outcrop of reef limestones from Snelslow to Bradwell Dale (fig.3). In western Derbyshire, the Upper Dovedale reef knolls of Parkhouse Hill and Chrome Hill (Hudson 1930a) have proved favourable collecting sites. Collecting from the Clitheroe reef-limestones of both the Coplow and the Salt Hill series (Parkinson 1926) has provided insufficient martinias and schizophorias for the purposes of the present analysis.

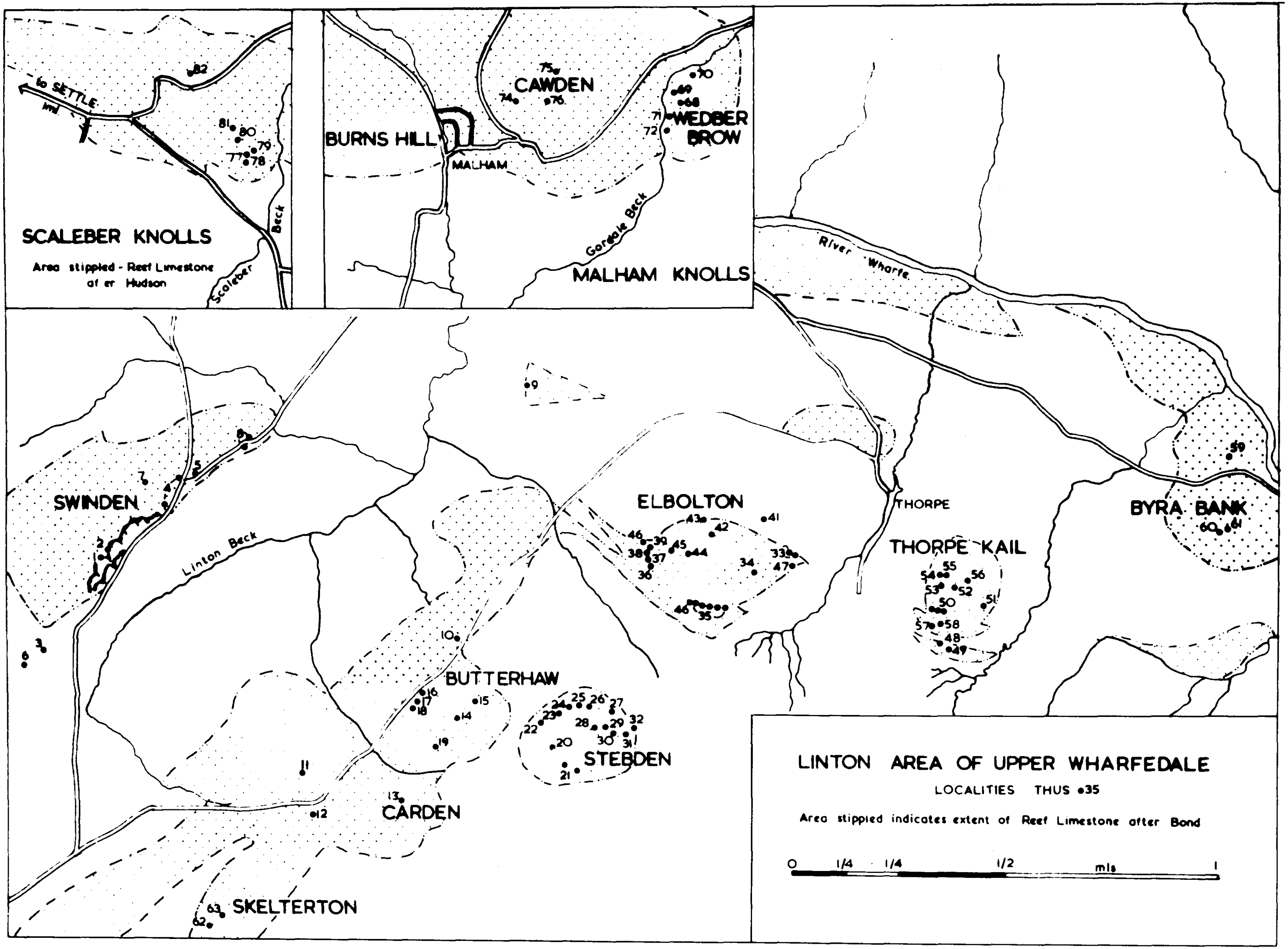


Fig.2.- Fossiliferous localities in the Craven reef limestones.

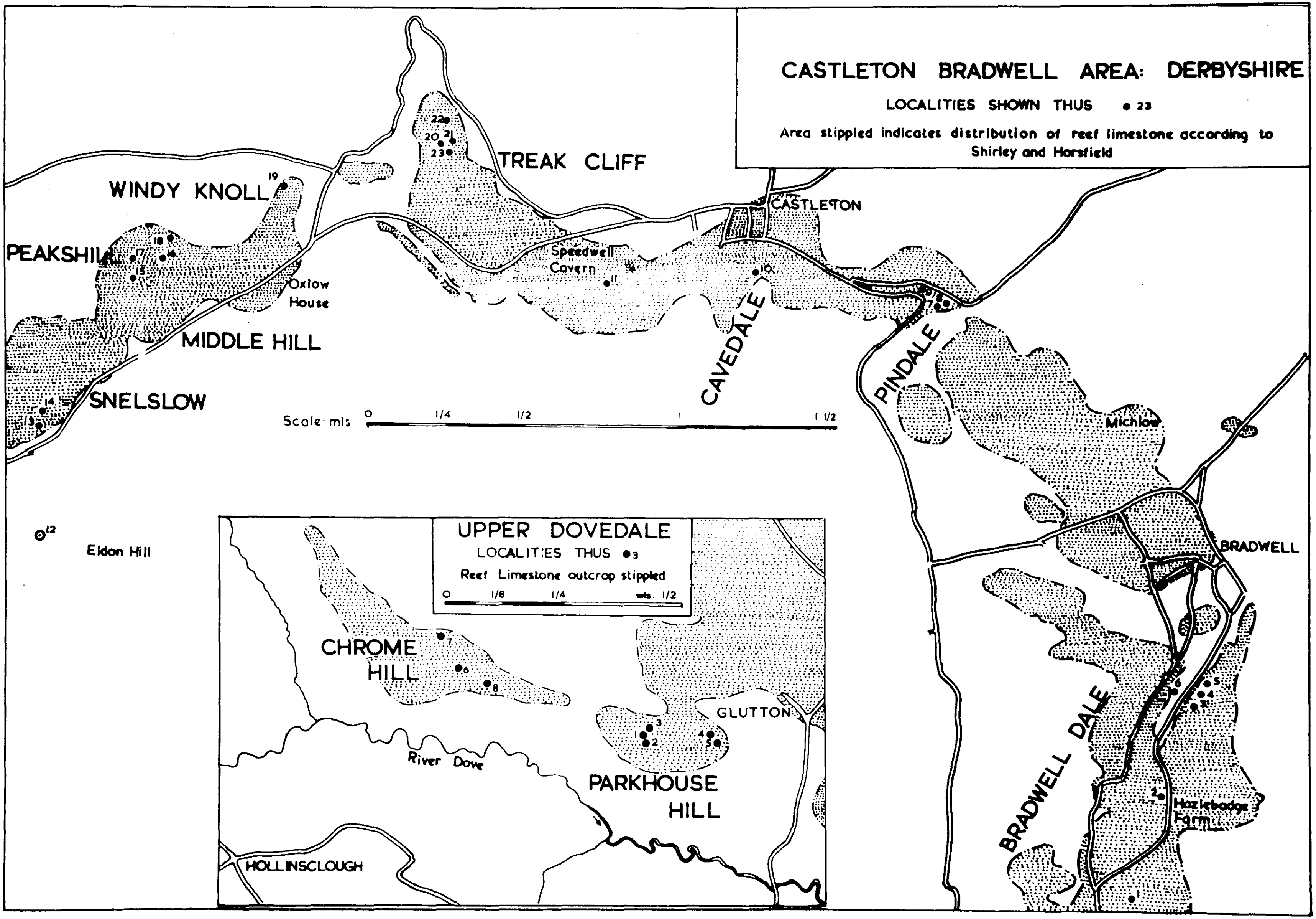


Fig.3.- Fossiliferous localities in the reef limestones of North Derbyshire.

Nature of the collecting. In general, the extent of the outcrops from which material has been collected is of the order of a few square yards. Where possible blocks of the more richly fossiliferous material have been collected for extraction of fauna in the laboratory. Some of the samples are composed of two or three sub-samples each of which has been derived from the break down of a single block of limestone. All localities have been recorded on six-inch maps, from which figs. 2 and 3 have been compiled.

Extraction of Fossils.

The similarity in chemical composition of matrix and shell material has precluded etching by hydrochloric acid as a means of extraction. Silicification, where it occurs, is incipient, never reaching the stage of selective replacement of the fibrous material of the shells. The use of hydrogen peroxide or alternate heating and cooling to separate shell from rock matrix is also ineffective. It merely results in damaging the contained specimens.

Mechanical crushing is the only suitable method which may be applied and collection of the total fauna is not possible. Nevertheless, samples have been extracted which may be considered representative of the original assemblages.

Preparation of Specimens and Study of Internal Structure.

Where complete individuals occur, especially of the biconvex forms, extraction presents no difficulty, particularly from weathered limestone. Little further preparation is required, apart from cleaning the hinge-lines.

Difficulty occurs when an attempt is made to investigate internal structure. Cast and mould structures are absent. Recrystallisation of the calcite infilling frequently distorts the internal calcified skeleton.

In some cases the shell may be removed by immersion in dilute hydrochloric acid and the muscle scars may then be seen. Occasionally the lophophore support is visible through the transparent calcite infilling when the opaque fibrous calcite of the shell has been removed. Calcining is not possible, the specimens becoming damaged when heated as the infilling calcite does not behave with sufficient homogeneity to resist stress.

Investigation of the internal structure by use of X-ray and gamma-ray sources has not been successful. Specimens of *Martinia* mounted on photographic plates, collimated with lead screens and subjected to irradiation from an X-ray source of from 20 to 80 keV for periods of from 4 to 20 seconds, have not yielded images. A source of greater penetration though lesser hardness than X-rays was provided by using radioactive cobalt (Co^{60}). Exposure for two days to radiation of approximately 1.25 meV again proved unsuccessful. There is obviously insufficient difference in structure between the calcite of the shell and brachial supports on one hand,

and that of the infilling on the other, to provide differential absorption of radiation and give an image on a photographic plate.

The most useful and accurate method of examining internal structure has been by use of serial sections. Cellulose peels have been prepared in the usual manner from lightly etched surfaces. Specimens have been mounted for this purpose in plaster of Paris or, more usefully, in Marco resin which being transparent enables a check to be kept on orientation (Cummings 1950).

Staining techniques have been attempted using Malachite green and Alizarine. Heeger's method using an acid solution of potassium ferricyanide has also been used (Henbest 1931). Although unsatisfactory on flat surfaces of hand specimens, such methods may be of greater use in thin section work. The cellulose acetate peel takes up the colour impregnating the limestone surface, although lack of selective staining between the coarse and fibrous calcite renders this of little value.

Selection of Fauna.

A great number of brachiopod species occur in the reef-limestones. Of these it has been found suitable to select Schizophoria resupinata and Martinia aff. glabra for the purpose of the present analysis. They occur in large numbers, they are widespread in their distribution, and they are frequently associated together.

Application of Statistics.

The reef faunas are abundant and even with localised collecting samples of moderate size are provided. The individuals comprising the samples are sufficiently alike to require finer analysis than is possible by qualitative methods. Statistical techniques are suitable.

A preliminary series of measurements has been made on a sample of schizophorias. Those measurements most suitable for analysis have been ascertained and, using them, a study has been made of variation within and between the samples.

The main statistical data employed are, the mean, standard deviation, standard error of the mean, the regression equation, the correlation coefficient, the partial regression equation, the F-test, t-test, analysis of variance, and discriminatory analysis.

Measurement.

In practically all cases sufficient accuracy has been given by the use of vernier calipers reading to 0.1 mm. For certain purposes, such as the measurement of the density of costellae on the surface of schizophorias, a micrometer eyepiece attachment to a normal monocular microscope has been suitable.

IV. GENERAL DESCRIPTION OF THE BRACHIOPOD FAUNAS.

The association of genera in the brachiopod faunas differs from one locality to another. This is shown by the following description of the general variation in these faunas from the principal localities, and is illustrated diagrammatically in fig.4.

Locality Y/35 (Elbolton, Yorkshire). The fossiliferous limestone pockets are largely a mass of martinia and productid shells lying together without any preferred orientation, and often closely associated with distorted orthotetid valves. The martinias are well preserved and are very often complete shells. In several cases a complete shell is found resting securely in the single valve of a slightly larger specimen. The bearing of this on the environmental conditions is discussed below. Encrusting layers of bryozoa spread over the shells and indicate an exact contemporaneity of the individuals comprising the assemblage.

Schizophoria, usually as single valves, occurs together with dielasmatids, phricodothyrids, costate rhynchonellids and a wide range of productid genera. Crinoid stems are present and a few small lamellibranchs and gastropods occur.

Locality Y/24 (Stebden, Yorkshire). The generic aspect of the fauna is similar. There are proportionately fewer examples of the partial enclosing of complete martinias by single valves of other specimens. Lamellibranchs are much

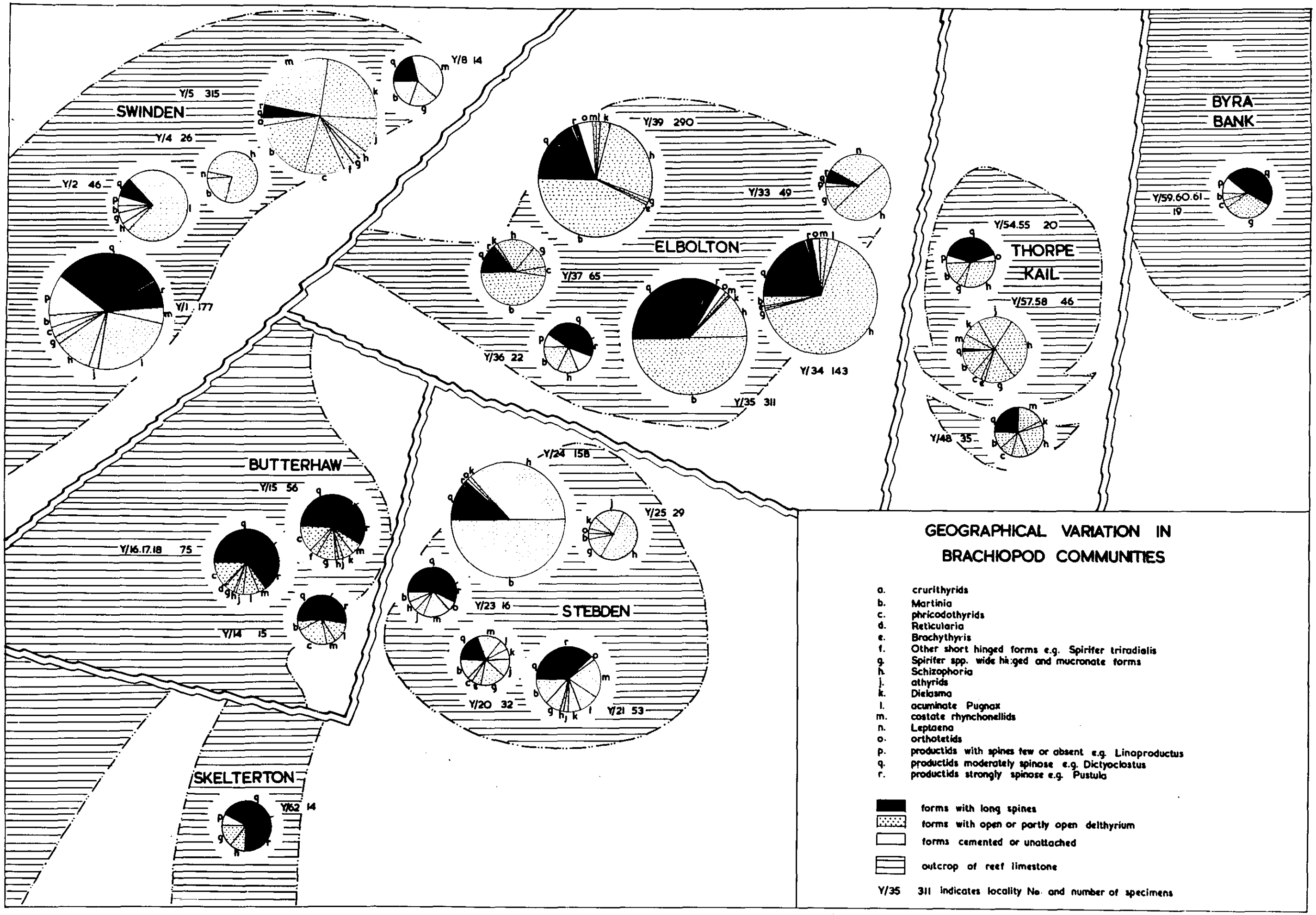


Fig.4.- Geographical variation in brachiopod communities in the Linton-Cracoe area of Craven.

more plentiful.

Locality Y/5 (Swinden, Yorkshire). The generic aspect shows considerable variation. The commonest genera are *Martinia*, *Dielasma*, and *Phricodothyris*, though a few *Schizophoria* are present. A wide variety of small, reflexed and incipiently ribbed rhynchonellids, a few larger smooth and a few larger costate rhynchonellids, occur. There are also some rectimarginate and some plicate athyrids, some costate and plicate spirifers, and a wide variety of productids. Apart from the variety of genera, the most striking feature of the fauna is that all the brachiopods are small. This may be due to sorting and is discussed below.

Locality D/21 (Treak Cliff, Derbyshire). The bulk of the fauna is composed of *Dielasma* and *Schizophoria*. Martinias are relatively few. One or two brachythyrids and other ribbed spirifers, and a few costate rhynchonellids, comprise the remainder of the fauna. Growth halts are unusually well developed in the brachiopods from this locality.

The main difference in the composition of the brachiopod fauna of the Treak cliff locality, as compared with those from the Yorkshire knolls, is a much higher proportion of *Dielasma* and a corresponding diminution in the quantity of *Martinia*. *Schizophoria* appears to be equally common in both areas.

The significance of these observations is discussed below in the light of studies on the distribution of modern mollusc faunas.

V. MORPHOLOGY.

(i) Schizophoria resupinata.

Many of the individuals examined resemble the illustration of Davidson (1857-62, pl.xxx, fig.1) though Bond (1941) makes no reference to this figure in his systematic study of the genus. The outline drawings given by George and Ponsford (1938, p.238, fig.10) are also similar to some of the more frequently recurring forms present in the samples studied. These two authors refer the drawings to Schizophoria cf. dorsosinuata Demanet, though Demanet's diagnosis of Schizophoria resupinata var.dorsosinuata (1934, p.53, pl.3, figs.14, 15) indicates that, as the name implies, the dorsal sinus is an integral part of the variety. Many of the specimens examined resemble Schizophoria woodi Bond, especially the form illustrated in Demanet (1934, pl.4, figs.1-3). Other specimens resemble S.palliata Demanet as figured by Bond (1941, p.298, fig.36) though the small angle of divergence of the dental lamellae which he figures has not been seen. It seems preferable in this study to retain the name Schizophoria resupinata.

Specimens from any given sample are variable especially in the depth of the shell. The interareas vary in their orientation. For the dorsal valve they may show any inclination from anacline to apsacline and for the ventral valve they vary from orthocline to procline (see Schuchert and Cooper 1932, p.20). In a few rare specimens the dorsal valve becomes extremely convex and the dorsal umbo high and incurved. The ventral valve in these individuals is correspondingly less convex and may be quite flat.

The ornament consists of fine radial costellae along certain of which a series of regularly spaced hollow spine bases may develop. In thin section punctae are quite prominent, penetrating to the exterior of exfoliated specimens.

Serial sectioning reveals the following details of the cardinalia. The cardinal process is usually bifid and strong shafted. One specimen (from Locality Y/34) shows a third ridge of equal prominence, though this may correspond merely to one of the auxiliary processes mentioned by George and Ponsford. Strong dental lamellae bound the delthyrium and swell anteriorly into very prominent bulbous teeth. The notothyrium is bounded by equally strong brachiophore plates which at hinge level bear triangular sockets. In some cases the ventral margin of the plates bounding the socket appears a little more posteriorly than the lateral margins. This means that the dental lamellae must bend forward as well as ventrally towards the sockets. Fulcral plates bounding the sockets connect them to the cardinal area. A median septum occurs in the ventral valve and is sporadically developed in the dorsal valve. In some partially exfoliated specimens from Locality D/21 the musculature is visible and, although a subdivision is possible of the ventral scars into divaricator bounding adductor, the presence of pedicle or adjustor scars cannot be ascertained. The area of divaricator and adductor appears to be more nearly equal than in the diagrams given by George and Ponsford (p.233, fig.5). The dorsal adductors bounded by the brachiophore plates and divided along part of their length by a median septum may be faintly distinguished.

In one of the larger specimens from Locality Y/34, the adductor scars closely resemble the dorsal musculature figured by George and Ponsford (p.230, fig.3a) for S.nuda.

A diagrammatic reconstruction of the species based on the serial sectioning of a number of individuals is given on fig.5.

(ii) Martinia aff.glabra.

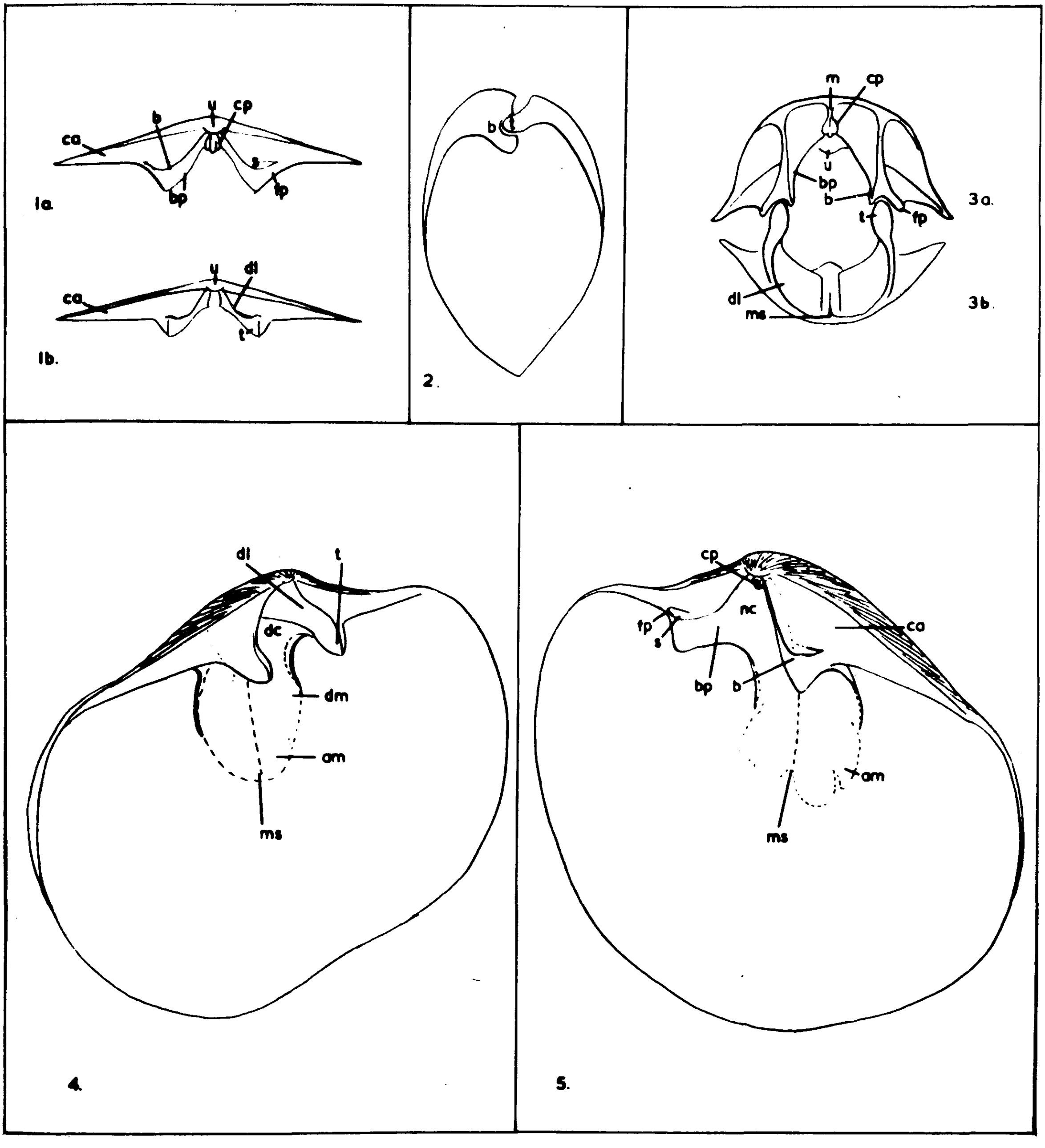
Individuals closely similar to the illustrations of Martin (1809, pl.48, figs.9, 10) and others resembling that figured by Phillips (1836, pl.x, fig.11) occur among the variable forms examined. Some of the specimens resemble Davidson's figures (1857-62, pl.xii, figs.1, 2, and cf. specimen showing linguoid plication pl.xii, fig.9).

Although usually wider than long, relatively narrow forms are not uncommon. The valves are fairly equally convex and the umbones moderately incurved. The hinge is shorter than the greatest width and the cardinal extremities

Fig.5: Diagrammatic reconstruction of *Schizophoria resupinata*.

Explanation:

am	adductor muscle
b	brachiophore
bp	brachiophore supporting plate
ca	interarea
cp	cardinal process
dc	delthyrial cavity
dl	dental lamella
dm	divaricator muscle
fp	fulcral plate
m	myophore of cardinal process
ms	median septum
nc	notothyrial cavity
s	socket
t	tooth
u	umbo



1. Cardinalia a. dorsal.
b. ventral.
2. Median section: lateral view.
3. Posterior view of cardinalia.
4. Ventral interior.
5. Dorsal interior.

Fig.5.- Diagrammatic reconstruction of the morphology of *Schizophoria resupinata*.

are rounded. Within a particular sample, individuals occur wherein the anterior margin varies from rectimarginate to strongly uniplicate, the plication itself varying from a gently curved flexure to a sub-rectangular fold. The surface is smooth, apart from growth lines, though some specimens possess a few inconspicuous widely spaced radial ridges. The shell is fibrous, and impunctate when exfoliated. The delthyrium is open or partly closed posteriorly by a small plate somewhat ventral of the interarea.

The following details are revealed by serial section. Plates directed obliquely to the floor of the ventral valve, and reaching one-third of the distance towards it, bound the margins of the delthyrium. Although not reaching the floor of the ventral valve, there is no reason why they should not be called dental lamellae as the function they serve is to support the teeth. This is at variance with the diagnosis given by George (1927, p.110). They increase in length when followed anteriorly. At the level of the hinge they are joined to narrow plates which swell anteriorly and dorsally into prominent teeth. The notothyrium is bounded by strongly curved plates with the concave margins opposed. They reach half way to the floor of the dorsal valve to which they are directed. At hinge level they extend a short way ventrally and form an effective margin to the sockets situated on either side of them. Anteriorly, the dorsal extremities merge into the lamellae which support the spires. The lamellae themselves are flattened dorso-ventrally initially but soon turn so that the flattening becomes lateral. They bear a short ventral projection before giving rise to the spires. There is no evidence of a jugum. The spire occupies most of the shell and is directed laterally. The posterior surface of the successive coils of the spire is almost parallel to the hinge, though in longer individuals the anterior surface may slope obliquely towards the cardinal extremities, giving a triangular appearance to each spire, seen in dorsal view. Eight or nine coils are usually present.

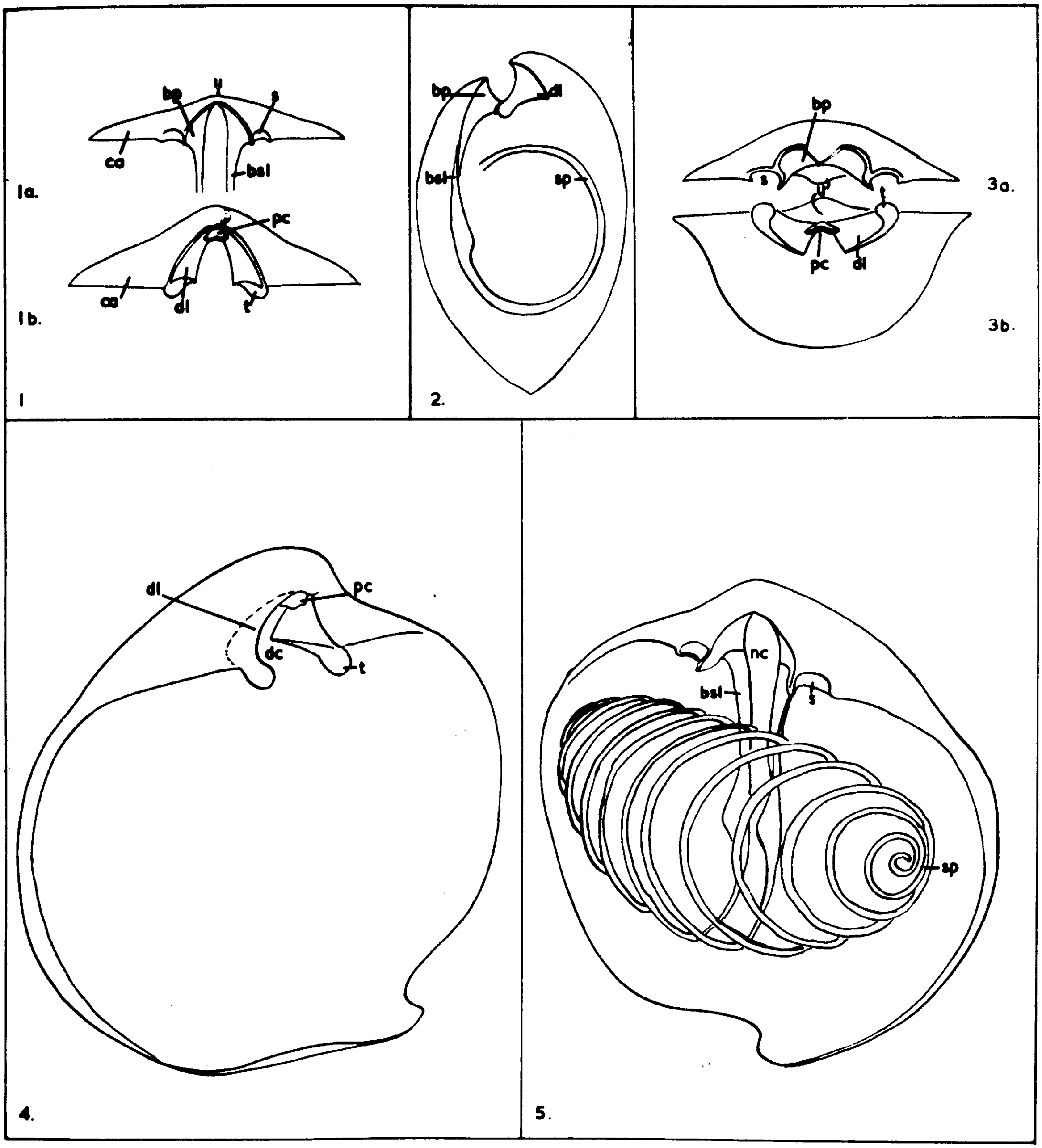
A diagrammatic reconstruction of the species based on the serial sectioning of a number of individuals is given in fig.6.

Fig.6: Diagrammatic reconstruction of

Martinia aff.*glabra*.

Explanation:

bp	brachiophore supporting plate
bsl	brachiophore supporting lamella
ca	interarea
dc	delthyrial cavity
dl	dental lamella
nc	notothyrial cavity
pc	plate which partly closes delthyrium
s	socket
sp	spire
t	tooth
u	umbo



1. Cardinalia a. dorsal view.
b. ventral view.
2. Median section lateral view.
3. Posterior view of cardinaliq
4. Ventral interior.
5. Dorsal interior.

Fig.6.- Diagrammatic reconstruction of the morphology of *Martinia* aff. *glabra*.

VI. ANALYSIS OF MEASUREMENTS.

A wide variety of measurements made on a selected sample indicates which kinds are most suitable for statistical analysis (see fig.7). The material comprising this sample is a group of 95 schizophorias from Locality Y/34 on the south face of Elbolton knoll, Yorkshire.

Length, width, and depth are easily and accurately determined. Hinge length may be measured with close approximation. Certain other features are conveniently measured indirectly by projecting lateral profiles of the shell using a point source of light. These are:

1. The distance of maximum thickness (depth) from the posterior.
2. The inclination of the ventral and dorsal interareas to the plane passing between the valves.
3. The degree of resupination.

The last of these is measured by dividing the shell profile by a plane normal to the anterior-posterior axis. The area posterior of this plane divided by that anterior of it, both areas considered ventral of the plane between the valves, is an approximate measure of the degree of resupination. This is explained in the accompanying figure where it is given by a/b.

The following summary of results emerges from the

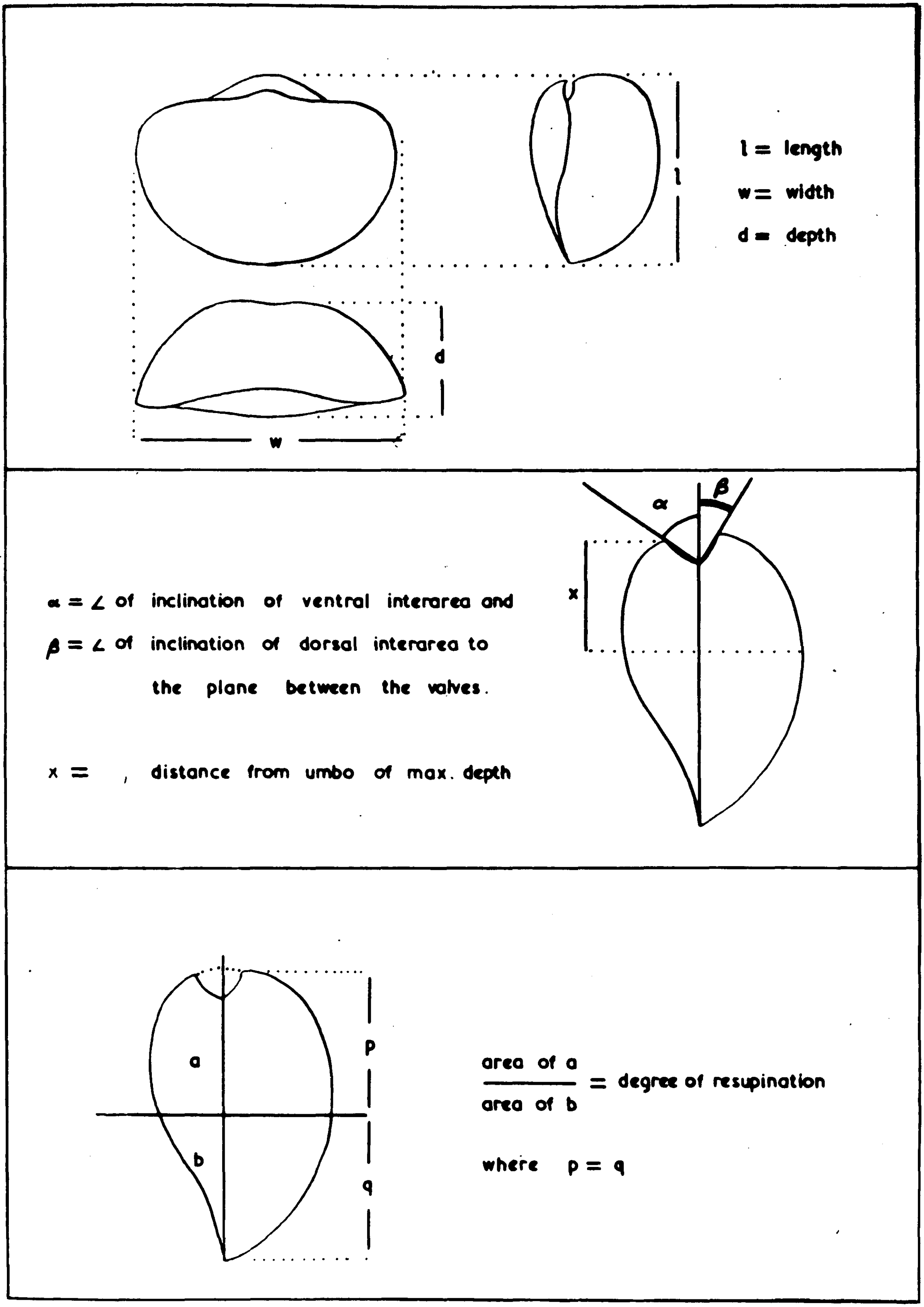


Fig.7.- Measurements used in the preliminary analysis of variation in schizophorias.

graphing of these several measurements.

1. Length, width, and depth show significant linear regression and a high degree of correlation when plotted against one another.
2. High correlation is also given by plotting the distance of maximum thickness from the posterior against length and depth.
3. The angle of inclination of the interareas and the degree of resupination do not show any significant regression against one another. Procline shells might be expected to show a greater degree of resupination, measured in the above manner, but this expectation is shown to be unjustified.
4. Distance of maximum thickness from the posterior, and the angle of inclination of the interareas do not show significant regression when plotted against one another, though again procline shells might be expected to have the position of maximum thickness situated more anteriorly than would those shells which are more orthocline. Absence of significant regression shows that this is not consistently true.
5. Frequency histograms have been constructed for the ratios width/length, depth/length, hinge-length/length, and distance from posterior of

the maximum thickness/length. All are distributed normally.

On the basis of the above analysis, it is evident that only those measurements noted under para.5 show a significant degree of correlation with one another. The ease and accuracy with which length, width, and depth may be determined relative to the other dimensions make these parameters of most value for a detailed statistical analysis. They are accordingly the measurements on which the main part of the present work is based, though note is taken throughout of such features as rib density, shape of anterior margin, inclination of interareas, resupination where present, and degree of divergence of the dental lamellae where observable (cf. Willard 1930). The rib density has been measured in one sample of 134 schizophorias. With the fine degree of costellation possessed by the schizophorias, application of the Bancroft ribbing formula is impracticable and has not been attempted.

Martinia is rather simpler in external structure. Length, width, and depth are conveniently measured. The degree of plication of the anterior margin does not vary directly with obesity, though young shells are usually rectimarginate. There is little variation in the inclination of the interareas to the plane between the valves, the shells are more or less uniformly biconvex and excepting growth lines the shell surface is quite smooth.

Certain features have been noted which may possess an environmental significance. They include the prominent growth halts of *Schizophoria*, the regeneration of shell material where damage has occurred to some specimens of *Brachythyris*, asymmetrical growth, and malformations of several shells of *Martinia*.

VII. VARIATION WITHIN SAMPLES.

Frequency Distributions.

The principal localities from which samples of martinias and schizophorias have been obtained are shown diagrammatically (figs.8, 9). The ratios of depth/length and width/length are plotted as frequency histograms. The standard deviation (s), mean ($\bar{x}$), number of individuals per sample (n), and the standard error of the mean ($s/\sqrt{n}$) are given for the frequency distributions from certain of these localities (Table I). In all cases the classes are taken as simple percentage intervals, no further grouping being attempted.

In place of grouping it is convenient to express the frequencies as cumulative percentages and plot them on Arithmetic Probability Paper (fig.10). On this scale a normal unimodal frequency distribution is represented as a straight line (Harding 1949). Thus comparison by inspection is possible and is less arbitrary than comparison of frequency distributions on normal arithmetic graph paper. Errors which may occur in the frequency histograms due to reading values to the nearest frequency class are minimised by the cumulative curve. The expression of the normally distributed curve as a straight line renders departures from it easily discernible.

The sharp rise which often occurs at the extremities of the curve (fig.10) is a feature which would diminish if the sample size were increased. Occurring as it does amongst

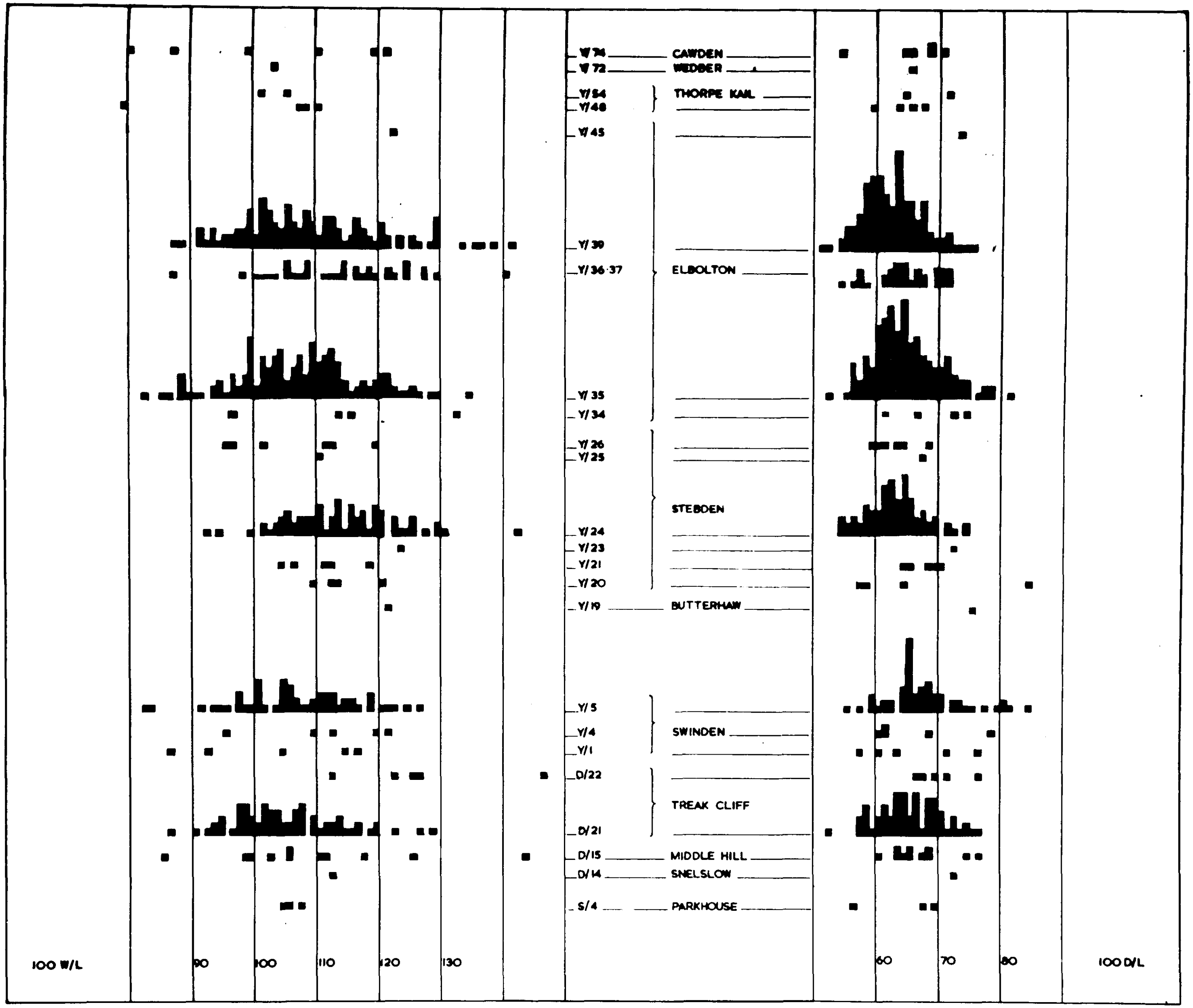


Fig.8.- Frequency histograms for width/length and depth/length ratios in samples of *Martinia*.

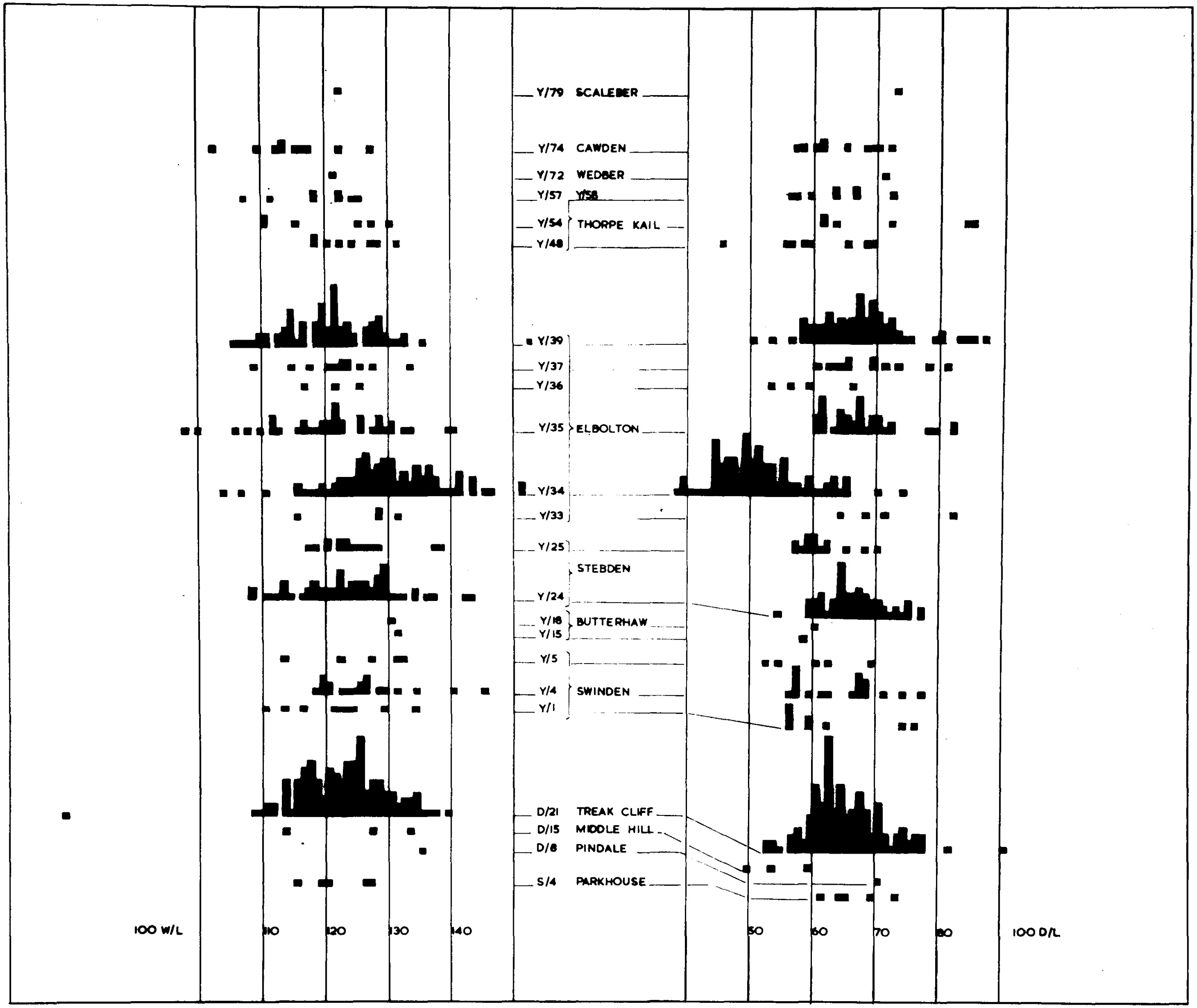
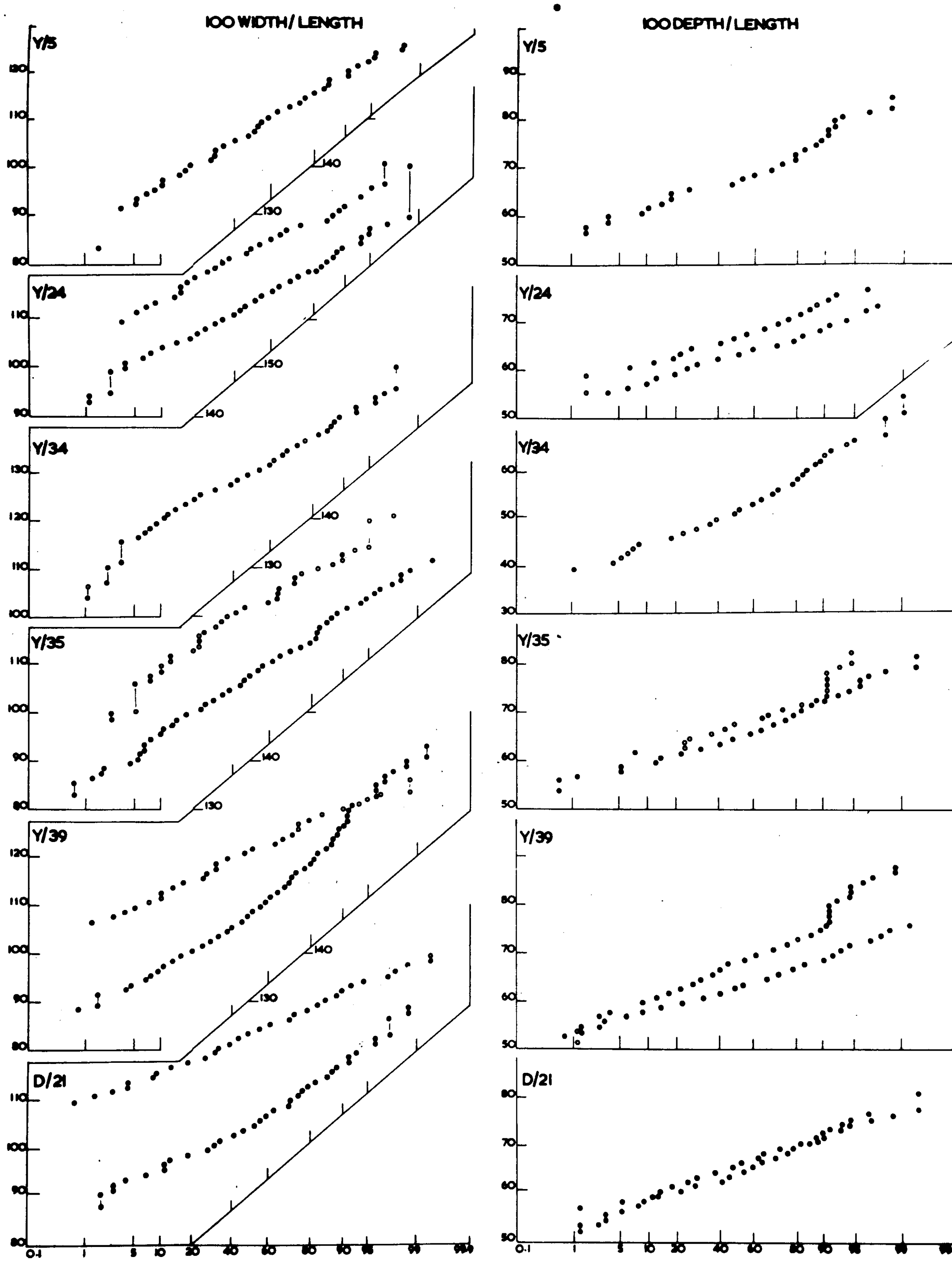


Fig.9.- Frequency histograms for width/length and depth/length ratios in samples of <u>Schizophoria</u>.



EXPLANATION :- Ordinates – percentage width/length and depth/length on arithmetic scale.
Abscissae – percentage cumulative frequency on probability scale.
Open circles – Schizophoria frequency.
Solid circles – Martinia frequency.
Localities Y/5 Swindon Y/24 Stebden Y/34 Y/35 Y/39 Elbolton. Yorks.
D/21 Treak Cliff Derbyshire

Fig.10.- Frequency distributions of figs.8, 9, represented on the arithmetic probability scale.

TABLE I

MARTINIA. 100 W/L.

	s	$\bar{x}$	n	$s / \sqrt{n}$
Loc. Y/5.	10.24	107.087	56	1.368
Y/24.	8.68	114.364	77	0.989
Y/35.	9.74	107.849	152	0.790
Y/39.	11.31	109.758	124	1.016
D/21.	8.48	105.521	71	1.006

SCHIZOPHORIA. 100 D/L.

	s	$\bar{x}$	n	$s / \sqrt{n}$
Loc. Y/24.	4.97	67.259	58	0.653
Y/34.	7.22	52.084	95	0.741
Y/35.	5.74	68.051	39	0.919
Y/39.	7.04	68.013	77	0.802
D/21.	5.71	65.642	137	0.488

the end members of the series it does not represent a departure from normality.

The depth/length ratio from Locality Y/39 alone shows such a departure, but as this is due to only five specimens it may be regarded as not being significant. There is then general uniformity amongst the samples which may therefore be regarded as random and representative of the original populations.

It is apparent that individuals of different sizes may possess similar proportions and it is therefore desirable to find out whether frequency distributions based on size show continuous variation.

The frequency distributions for shell length have been plotted on the probability scale, and they show general uniformity. One sample, that from Locality Y/24, departs from normality. It shows a group of large individuals present amongst a majority of somewhat smaller ones. The form of the frequency polygon is shown in fig.11. It is evident that a second less prominent mode occurs among the larger individuals. As Percival (1944, fig.1) indicates, such subsidiary modes may occur in life assemblages and their presence may therefore imply little more than a lack of sorting. The cumulative frequency curve compares with those curves obtained for poorly sorted sediments. There is then insufficient evidence to treat the anomaly shown by sample Y/24 as indicating heterogeneity within this assemblage.

Day (1915) has demonstrated a progressive shifting of the mode of frequency polygons based on ratio measurements of Reticularia lineata (Martin). They show an increase of length relative to width, and to depth with increasing size. An estimate from Day's graphs of this movement from the lowest to the highest size class is small, being approximately one half of the standard deviation.

In the present work, the high degree of correlation demonstrated (see below) between length, width, and depth, and the closeness with which some of the high values approach the regression lines, is evidence that there is little change of proportions with increase of size. This is further supported by the approach to isogonic growth shown by Treak Cliff martinias (fig.14). The above considerations have been thought necessary for, in order to retain samples of fairly large size, they have not been divided into size classes.

A further consideration remains. If a population has not been moved from the area in which it lived then any random sample will be representative of it. In the examples studied, however, it is evident that the shells are not now found where they once lived. Movement of the population must have occurred, and before examination of variation can be undertaken it is essential to know more about this movement. Its amount will be shown by the degree of mixing or sorting encountered in the samples.

Sorting.

Inspection of frequency distributions based on particle size is a convenient way of comparing the degree of sorting present in different sediments. In the present case, the 'particles' are represented by brachiopod shells. Features of importance in the frequency distributions, from the point of view of sorting, are the range and the spread which is best measured by the standard deviation.

In samples of Martinia from five different localities, the frequency polygons, based on measurement of length, are as shown (fig.11) and the main statistical data of these distributions is tabulated (Table II).

The degree of sorting is higher in the Derbyshire locality than in those from the knolls of Elbolton and Stebden in Yorkshire. The case of Y/5 is anomalous since, as inspection shows, only small individuals are represented. As all the brachiopod genera of this locality are small, they may represent the outcome of very efficient sorting. Furthermore, the concentration of large globose specimens of Schizophoria in Locality Y/33, may be another indication of such sorting.

One further consideration indicates that sorting is in fact the main cause of the size difference between the

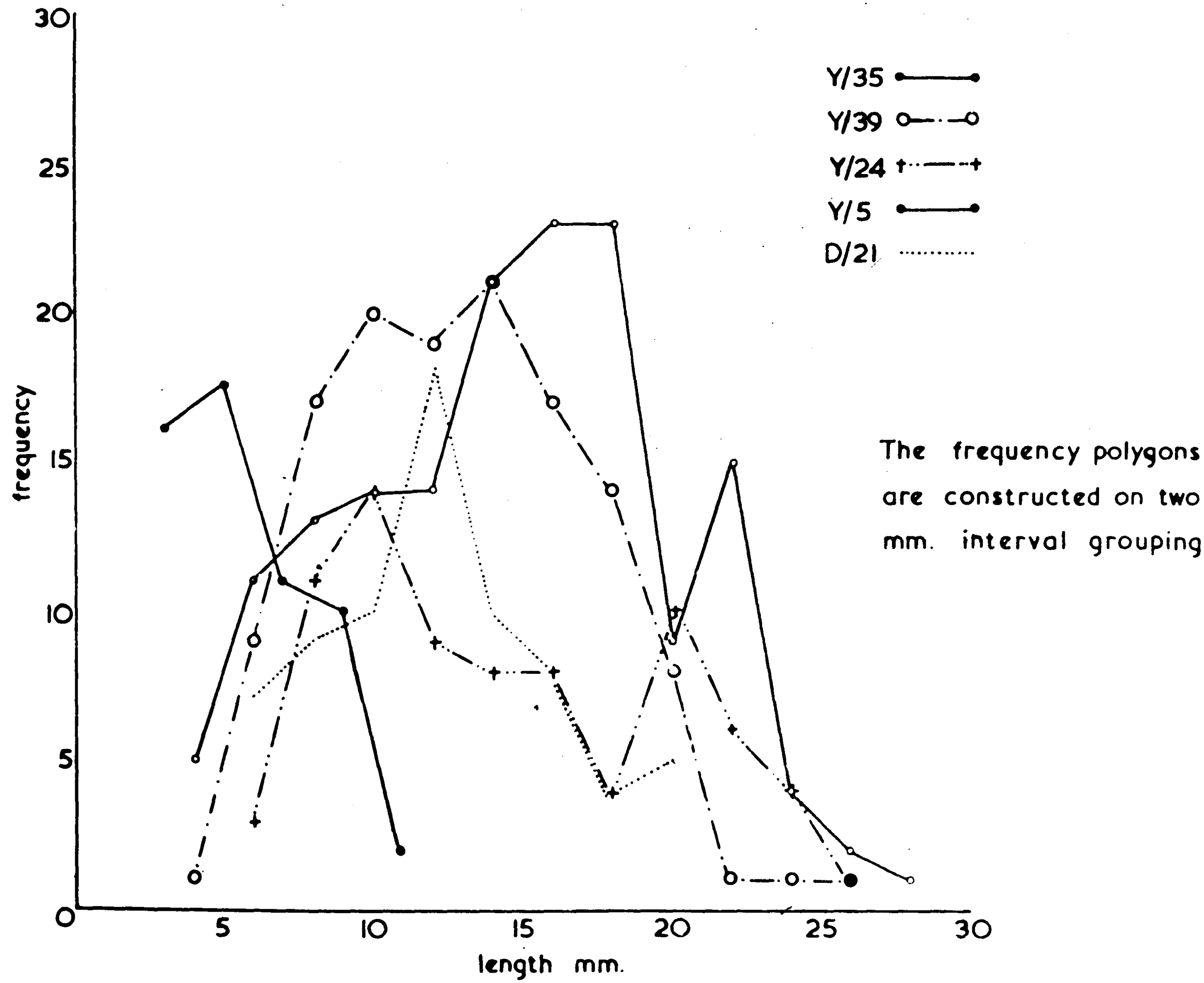


Fig.11.- Frequency polygons for samples of Martinia from selected localities.

TABLE II

Statistics for frequency distributions based on length of martinias.

		s	$\bar{x}$	n	$s / \sqrt{n}$
Loc.	Y/5.	2.29	5.64	56	0.306
	Y/24.	5.06	14.70	79	0.569
	Y/35.	5.42	14.65	155	0.435
	Y/39.	4.37	12.89	129	0.385
	D/21.	3.82	12.11	71	0.453

sample from Locality Y/5 and those from other localities. Comparison may be made between the frequency polygon for the sample from Y/5 and that of the normal unsorted population shown by Percival (1944, p.3, fig.1). The frequency polygons in Percival's figure are based on the length and breadth of a modern species-assemblage. They show marked positive skewness indicating a large number of small individuals and a rapidly decreasing number of larger ones. The frequency polygon for Y/5 differs in that the larger individuals are completely absent. The remaining frequency polygons under consideration differ from Percival's in the absence of marked positive skewness.

The orientation of the shells of Martinia is random throughout the material examined and in many cases isolated valves occur. As indicated above, a complete Martinia is frequently found cradled in the single valve of a slightly larger specimen. Matrix material seldom occurs between the single valve and the complete shell. Usually it is completely absent. The common occurrence of such cases demands a winnowing by moving water. The perfection of fit shown by the absence of matrix material indicates that movement must have been fairly persistent. If a complete shell became lodged in the single valve of a much larger specimen it would not stay there but be moved out and the process repeated until a more exact fit resulted.

The movement of terebratulid shells has been investigated in tank experiments by Menard and Boucot (1951). They show that a large hollow shell of this type may often be more easily moved than quartz grains on a fairly rigid substratum. The relative density is the factor determining the ease with which movement will occur. On a sandy bottom, however, the quartz grains often move first and the shell settles down in the sand and may in this way become at least partially buried.

Thus the nature of the substratum is of importance as it may modify the degree of sorting. By thin section analysis (see below) the nature of the substratum in which the shells have finally come to rest before burial, has been determined. As is subsequently shown, the limestone of the Elbolton localities is extremely fine-grained, tending towards a calcite mudstone. On such a substratum movement might be impeded and is not likely to result in the shells being transported great distances before burial. The same is true of the Treak Cliff locality, though here the presence of grain limestone and occasionally of coarse shell fragment limestone provides a greater lithological variability. Grain and shell fragment limestones are common in Locality Y/5 and the amount of calcite mud is subordinate.

These observations fit in well with the degree of scatter of the frequency distributions which indicate a fairly high degree of sorting in Locality Y/5 and a much lower one in the Elbolton localities.

In conclusion, Vaughan (1940) may be quoted, "... the admixture of organisms of different environments ... is not of so frequent occurrence as to be very perturbing in the study of most fossil faunas".

Continuous Variation in Schizophorias.

The range of variation shown by the frequency histograms is illustrated in greater detail in fig.12.

A sample of 136 Schizophoria from Locality D/21 on Treak Cliff near Castleton, Derbyshire has been examined. The most variable dimension is the depth of the shell, and the pictograph is based on the ratio depth/length. The form of the distribution on the arithmetic probability scale is also shown.

Representative specimens of the series are figured in two aspects, both of which illustrate the variation in depth. They clearly indicate continuously increasing obesity. That the frequency is normally distributed is shown by calculating the statistics g_1 which is a measure of skewness and g_2 which is a measure of kurtosis (cf. Snedecor, p.174f). Dividing g_1 and g_2 by their standard errors s_{g_1} and s_{g_2} respectively, a t-test may be performed. The test of significance is carried out with an infinite number of degrees of freedom, the 5% level of t being 1.96.

The relevant figures are as follows:

$$t_1 = g_1 / s_{g_1} = 1.709$$

$$t_2 = g_2 / s_{g_2} = 0.0025$$

They show that there is no significant deviation from normality, both being below the 5% significance level. Thus the histogram may be considered as representing a normal frequency distribution and the variation in the schizophorias, at least in so far as depth/length is concerned, is a continuous one.

The specimen figured in inset lies outside of the range of continuous variation, its inclusion in the t-test considerably altering the values of t_1 and t_2 which become 34.932 and 3.646 respectively (n=137).

With the aid of a micrometer eyepiece the number of ribs occurring per mm. at a fixed distance from the ventral umbo may be measured. The results are as follows:

No. of ribs/mm. at 5 mm. from ventral umbo.	4	5	6	7	8
Frequency	9	41	59	23	2

They appear to be normally distributed. It may be noted that Bond (1941) separates two groups of <u>Schizophoria</u> species using rib density as his criterion. No such separation is possible on the basis of the above measurements, especially since the distribution is unimodal and high-peaked. Rather does this distribution serve to strengthen the evidence that the specimens of <u>Schizophoria</u> represent members

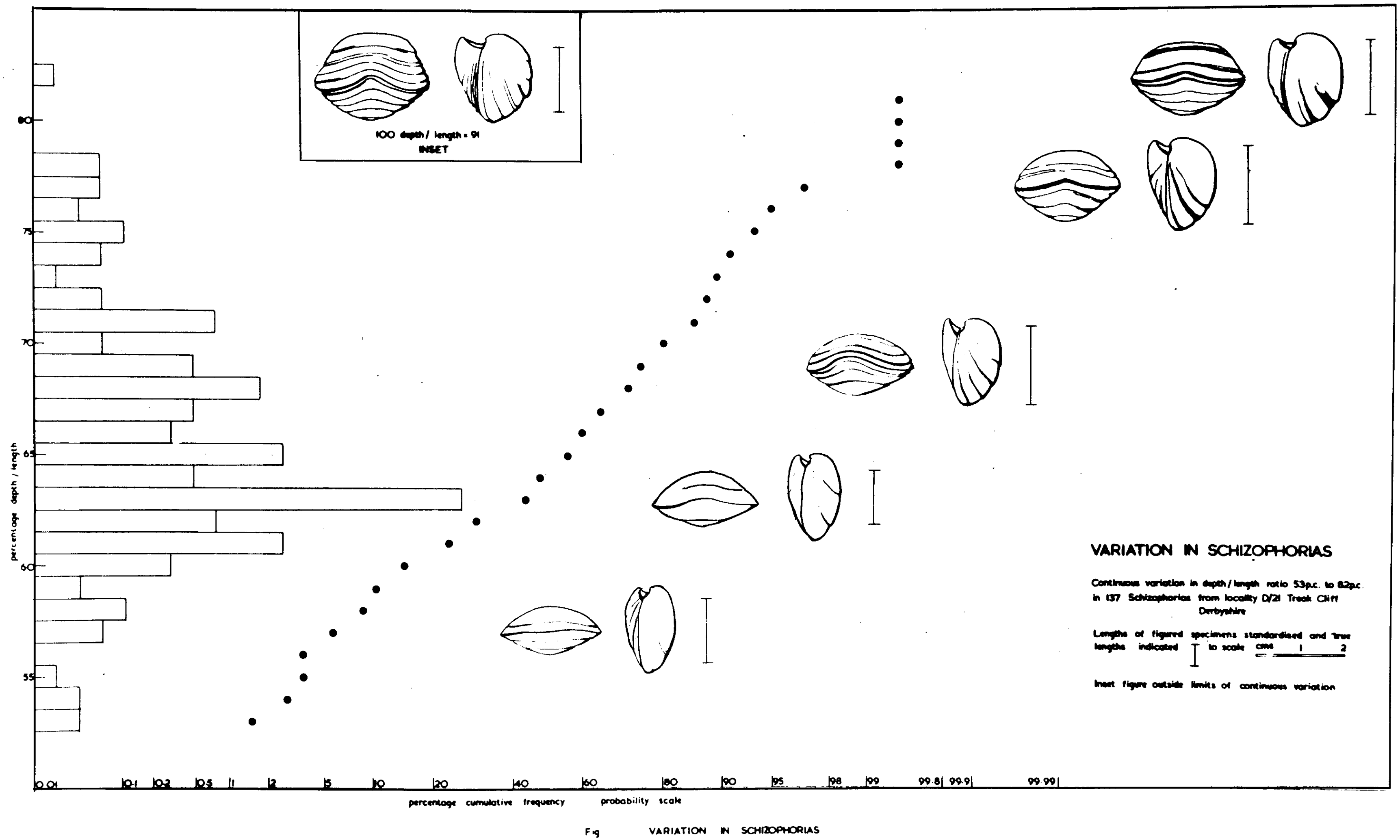


Fig.12.- Continuous variation in schizophorias from Locality D/21 Treak Cliff, Derbyshire.

of a series which shows continuous variation. It thereby emphasises the conspecific nature of the individuals.

Continuous Variation in Martinias.

A sample of martinias from Locality Y/35 on the south face of Elbolton Knoll, Yorkshire has been examined. In this case it was found suitable to pay particular attention to the width/length ratio, as showing the greatest degree of variation.

As in the case of schizophoria, the ungrouped frequency histogram and the curve on the probability scale are shown (fig.13).

A statistical analysis to test normality is not repeated, the form of the curve on the probability scale being taken as sufficient evidence that variation is continuous. Seven per cent of the sample may actually fall outside a normal distribution as exemplified by the narrow specimen figured, the hinge of which is fairly short and the cardinal angles highly oblique. Specimens such as this are not malformed as perfect symmetry is retained. It is interesting to note that present day pedunculate forms of the terebratulaceae are not dissimilar in general outline — a factor which probably allows of close crowding in communities (cf. Percival 1944).

Another factor of interest is the lack of correlation between height of plication and relative width. Some of the middle members of the series have quite strong linguoid plications. Although detailed analysis has not been made, there is nothing to suggest a high degree of correlation between depth of shell and height of plication. Very small shells, however, are usually rectimarginate.

As shown subsequently, there is a very high correlation between length, width, and depth. Again, therefore, it seems justifiable to include all specimens in the frequency histograms. Supporting evidence for this is derived from several of the Martinia from Locality D/21 Treak Cliff. These show quite well developed growth lines. With the aid of a micrometer eyepiece, measurement of the shell at different stages of growth can be made. The result is shown in fig.14. Growth appears to be sufficiently isogonic to permit of the assumption that there will be no significant departure from the proportion represented by a given regression equation.

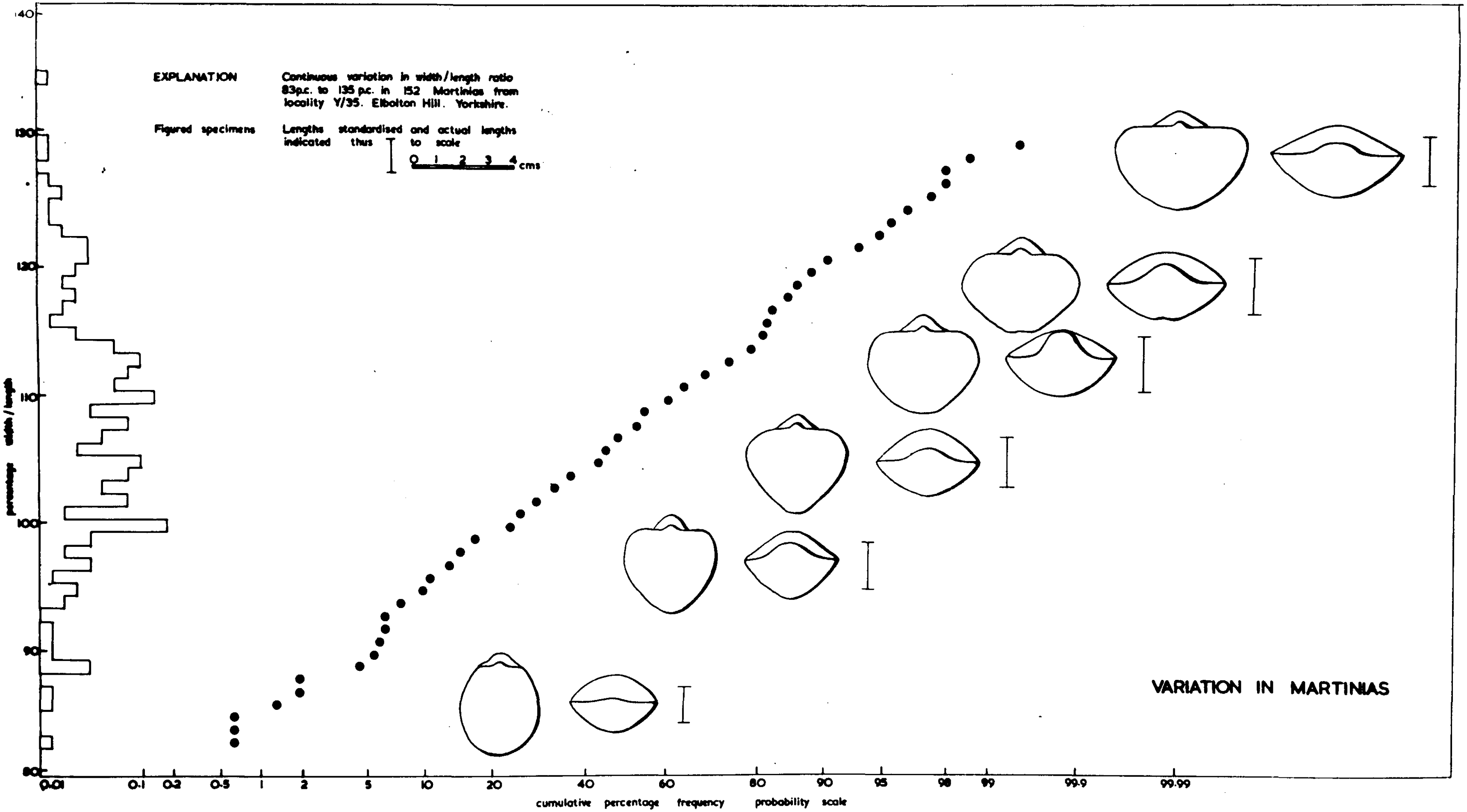


Fig.13.- Continuous variation in martinias from Locality Y/35 Elbolton, Yorkshire.

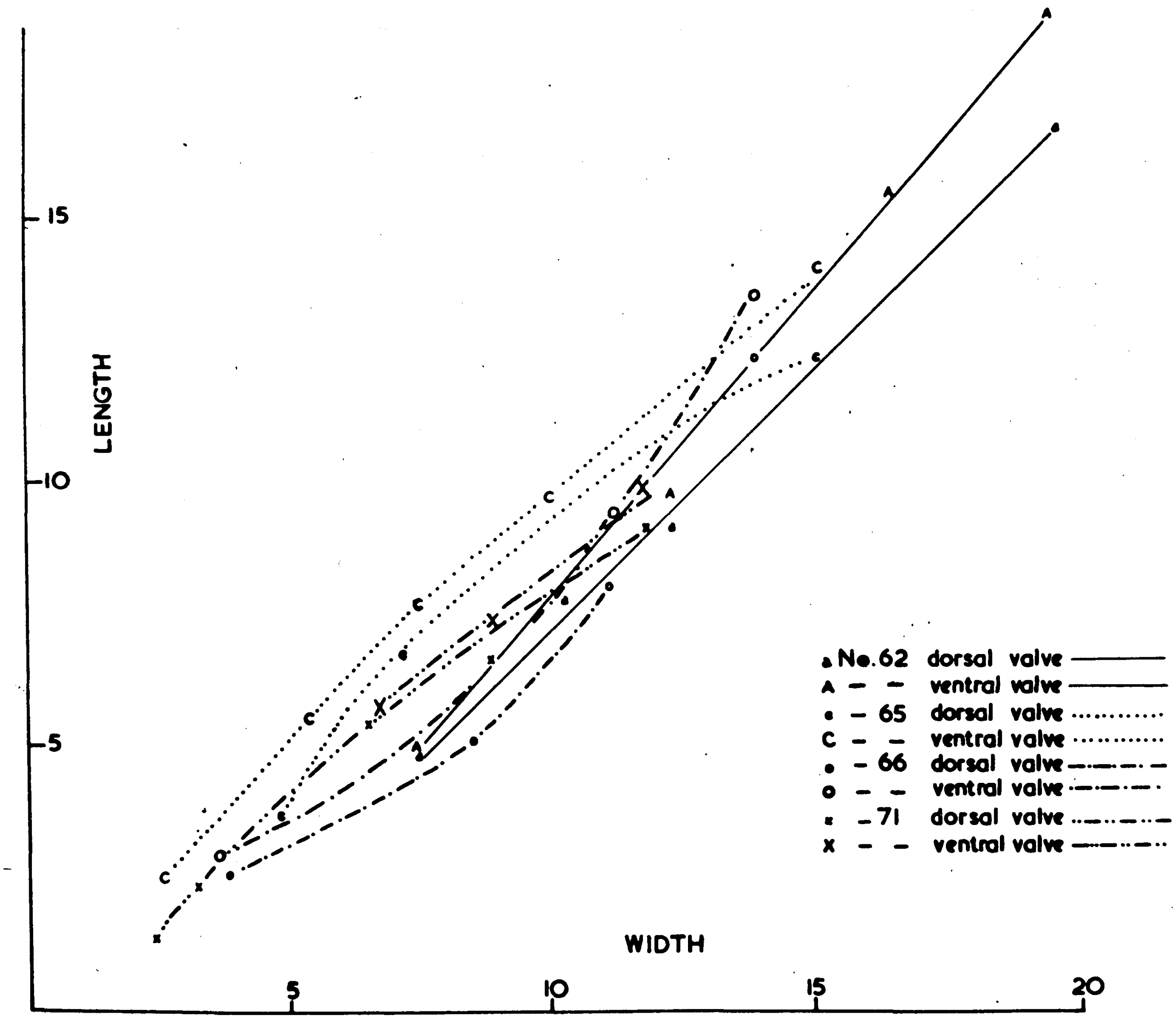


Fig.14.- Growth curves for martinias from Locality D/21 Treak Cliff, Derbyshire.

VIII. VARIATION BETWEEN SAMPLES.

The main purpose of the statistical analysis is treated in this section. Samples taken from different localities are compared on the basis of the measurements already described.

Linear Regression and Correlation.

The first method of comparison is by use of regression lines and correlation coefficients. Strictly speaking, the name "regression" should not be applied. The regression of one set of values on another implies that the latter are in some way causal, and the former values result from them. In the measurements analysed, each set of values has the same status. They may, however, be manipulated as regression lines.

The samples selected for analysis are determined by quantity of material and by location. Samples of *Martinia* are taken from three separate "knolls", viz. Elbolton, Stebden and Swinden all in Yorkshire. *Schizophoria* samples are taken from the same Elbolton and Stebden localities and from Treak Cliff in Derbyshire.

Length is plotted against width and against depth, and the two latter against one another, on normal arithmetic graph paper. Inspection is sufficient to show that a straight line will best fit the points (see figs.15-21 and Tables III, IV).

The large number of cases in which the exponential curve best fits organic growth (Huxley 1932) leads to a critical view of linear regression as best explaining growth in a particular case. It may be that were larger members present the curve would depart from linearity. However, no significant departure occurs from linear regression in this case and the high correlation substantiates the goodness of fit.

It can be seen that discrepancies between samples are exceedingly small. In some cases, particularly the length/width regression of Schizophoria from Y/24 and D/21, the regression lines practically coincide. It is perhaps the more surprising in that wide geographical distribution is involved. The regression lines for Schizophoria consistently show a greater variation between the samples from Elbolton Knoll and Stebden localities, 750 yards apart, than in the case of Stebden and Treak Cliff localities separated by 75 miles.

The same consistency does not hold in the case of the regression lines for Martinia. In length/depth ratio Y/24 and Y/35 compare closely. In width/depth ratio Y/35 is most closely comparable with Y/5.

The coefficients of correlation are remarkably high and very uniform, varying in eighteen examples from a minimum value of 0.943 to a maximum of 0.990. For convenient comparison they are plotted on a truncated scale shown in the accompanying graph (fig.22). Consideration of the

Martinia samples shows the same general pattern of correlation in each case. Whenever width is involved in measurement the correlation coefficient is relatively low. This means that width is the most variable of the three dimensions. The calcified spiral arms of *Martinia* are directed along the width axis practically parallel to the hinge. It is to be expected in that slight environmental changes would be reflected in the disposition and extent of the lophophore and the brachia which bear it. A slight change in conditions would presumably lead to a change in length of lophophore and a corresponding change in the width of the shell. The greatest variable in *Schizophoria*, again consistently so, is the depth of the shell.

TABLES III, IV

LINEAR REGRESSION AND CORRELATION

Mean values: $\bar{l}$, $\bar{w}$, $\bar{d}$.

Corrected sums of squares:

$$\Sigma l^2; \quad \Sigma w^2; \quad \Sigma d^2.$$

Corrected sums of products:

$$\Sigma lw, \quad \Sigma ld, \quad \Sigma wd.$$

Number of observations n.

Regression of W on L given by:

$$W = a + bL$$

$$\text{where } b = \Sigma lw / \Sigma l^2$$

Coefficient of correlation:

$$r = \Sigma lw \Big/ \sqrt{(\Sigma l^2)(\Sigma w^2)}$$

TABLE III

MARTINIA. Locality Y/35. N = 155.

$\bar{l}$ = 14.583	$\bar{w}$ 15.721	$\bar{d}$ = 9.674
Σl^2 = 4570.64	Σw^2 6049.72	Σd^2 = 2545.22
Σlw = 5100.65n	Σld = 3352.24	Σdw = 3817.43

W = -0.55 + 1.12 L.

r = 0.970

D = -1.02 + 0.73 L.

r = 0.983

D = -0.25 + 0.63 W.

r = 0.973

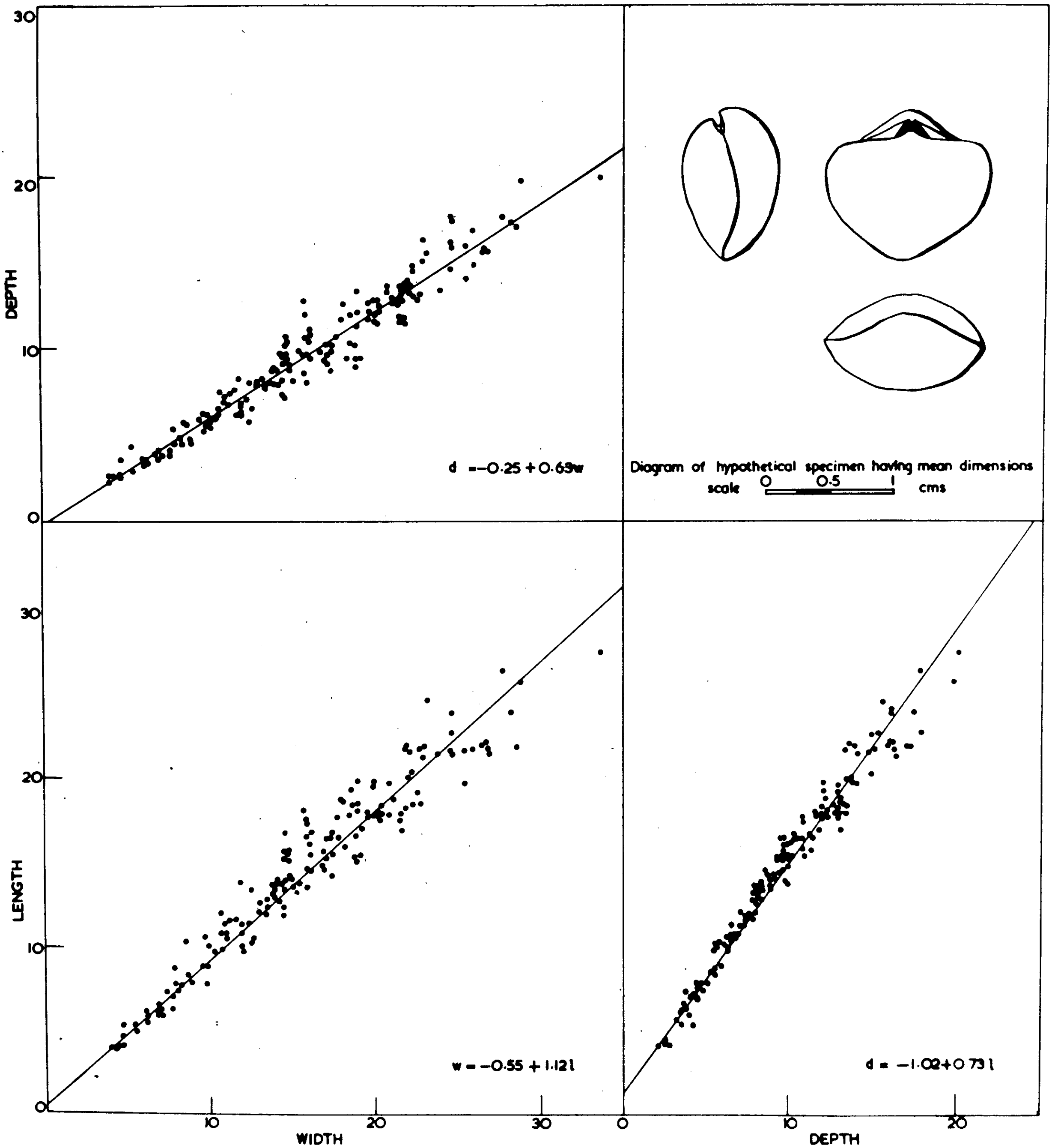


Fig.15.- Scatter diagrams for martinias from Locality Y/35 Elbolton, Yorkshire.

MARTINIA. Locality Y/24. $n = 79.$

$\bar{l} = 14.551$	$\bar{w} = 16.696$	$\bar{d} = 9.375$
$\Sigma l^2 = 2310.04$	$\Sigma w^2 = 3283.21$	$\Sigma d^2 = 1175.55$
$\Sigma lw = 2697.47$	$\Sigma ld = 1627.36$	$\Sigma dw = 1924.83$

$W = -0.30 + 1.17\ L.$

$r = 0.979$

$D = -0.88 + 0.70\ L.$

$r = 0.987$

$D = -0.41 + 0.59\ W.$

$r = 0.980$

MARTINIA. Locality Y/5. n =

$\bar{l} = 5.655$	$\bar{w} = 6.041$	$\bar{d} = 3.827$
$\Sigma l^2 = 280.22$	$\Sigma w^2 = 312.88$	$\Sigma d^2 = 121.81$
$\Sigma lw = 290.19$	$\Sigma ld = 181.72$	$\Sigma dw = 189.48$

$W = 0.18 + 1.04\ L.$

$r = 0.981$

$D = 0.16 + 0.65\ L.$

$r = 0.984$

$D = 0.17 + 0.61\ W.$

$r = 0.971$

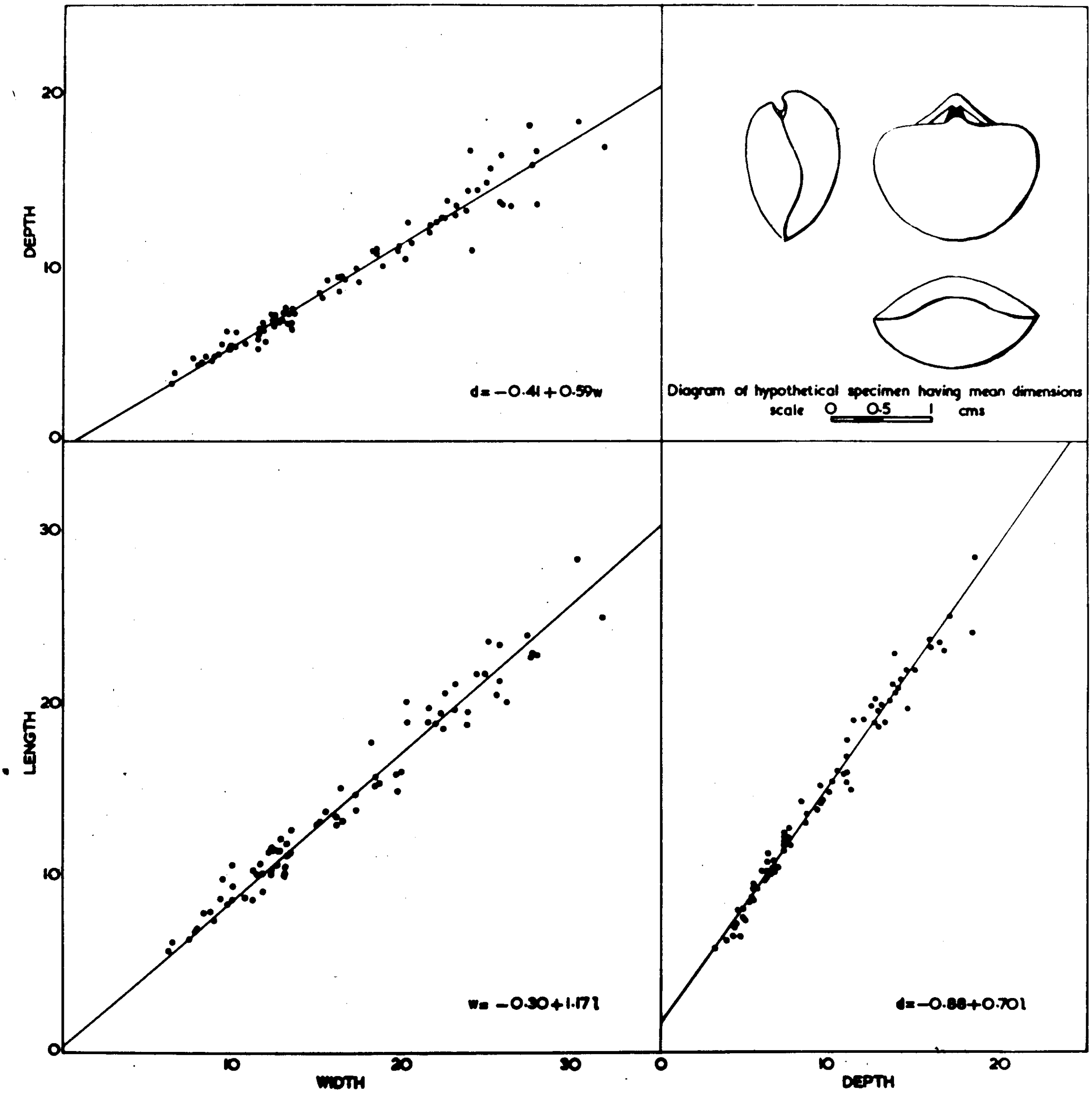


Fig.16.- Scatter diagrams for martinias from Locality Y/24 Stebden, Yorkshire.

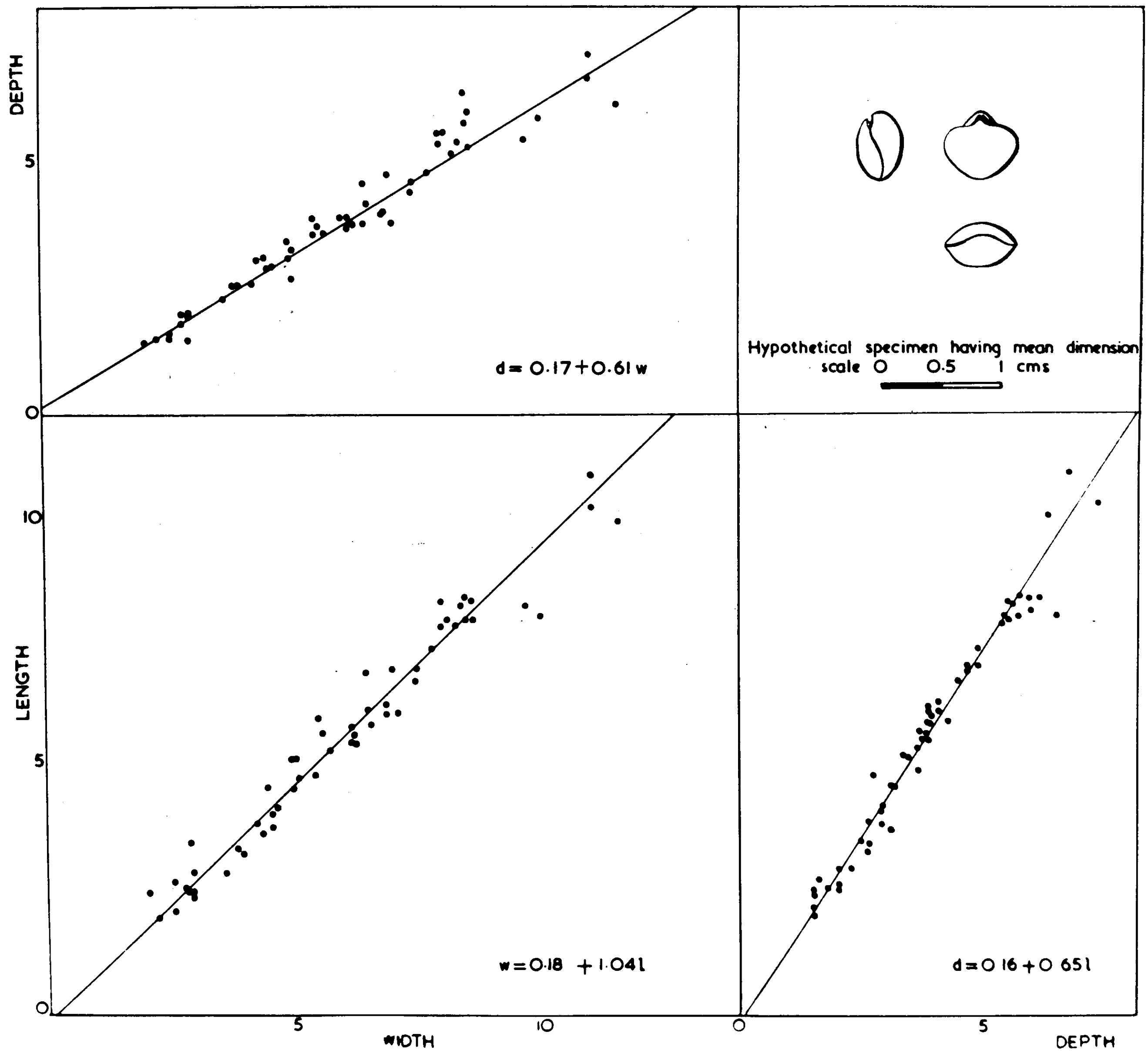


Fig.17.- Scatter diagrams for martinias from Locality Y/5 Swinden, Yorkshire.

TABLE IV

SCHIZOPHORIA. Y/35. n = 39.

$\bar{l}$ =	10.49	$\bar{w}$ =	12.72	$\bar{d}$ =	7.22
Σl^2 =	395.14	Σw^2 =	589.33	Σd^2 =	252.93
Σlw =	467.17	Σld =	305.92	Σdw =	364.20

$W = 0.33 + 1.18\ L$

$r = 0.968$

$D = -0.90 + 0.77\ L$

$r = 0.968$

$D = -0.64 + 0.62\ W.$

$r = 0.943$

SCHIZOPHORIA. Y/24. n = 58.

$\bar{l}$ =	9.793	$\bar{w}$ =	12.219	$\bar{d}$ =	6.609
Σl^2 =	412.72	Σw^2 =	708.61	Σd^2 =	234.55
Σlw =	525.63	Σld =	302.17	Σdw =	386.26

$W = -0.26 + 1.27\ L$

$r = 0.972$

$D = -0.56 + 0.73\ L$

$r = 0.971$

$D = -0.05 + 0.55\ W.$

$r = 0.948$

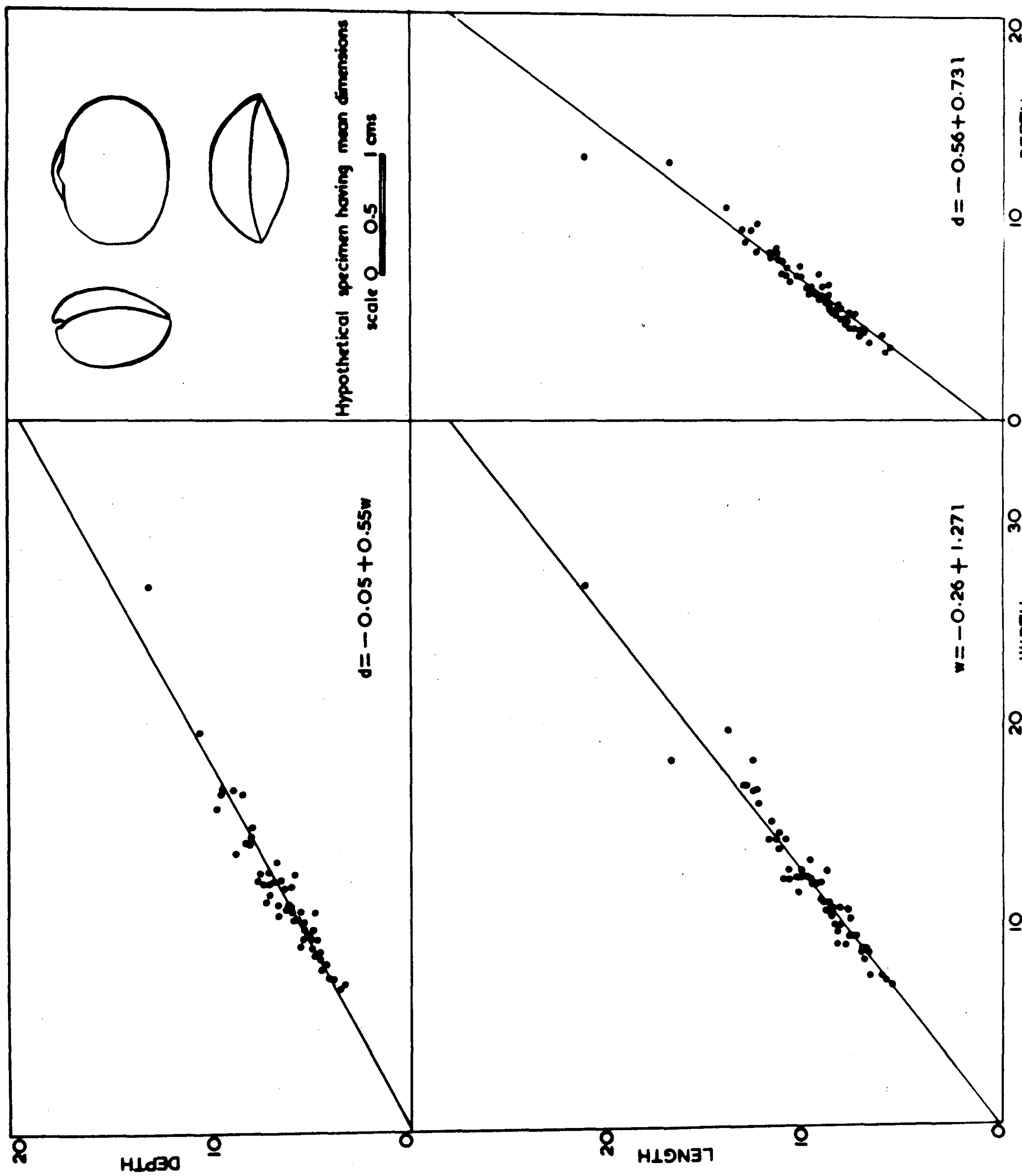


Fig.19.- Scatter diagrams for schizophorias from Locality Y/24 Stebden, Yorkshire.

SCHIZOPHORIA. D/21. n=137.

$\bar{l}$	=	9.709	$\bar{w}$	=	11.991	$\bar{d}$	=	6.504
$\sum l^2$	=	2012.63	$\sum w^2$	=	3165.91	$\sum d^2$	=	1118.70
$\sum lw$	=	2500.29	$\sum ld$	=	1459.99	$\sum dw$	=	1830.06

$W = -0.06 + 1.24\ L.$

$r = 0.991$

$D = -0.54 + 0.73\ L.$

$r = 0.973$

$D = -0.43 + 0.58\ W.$

$r = 0.972$

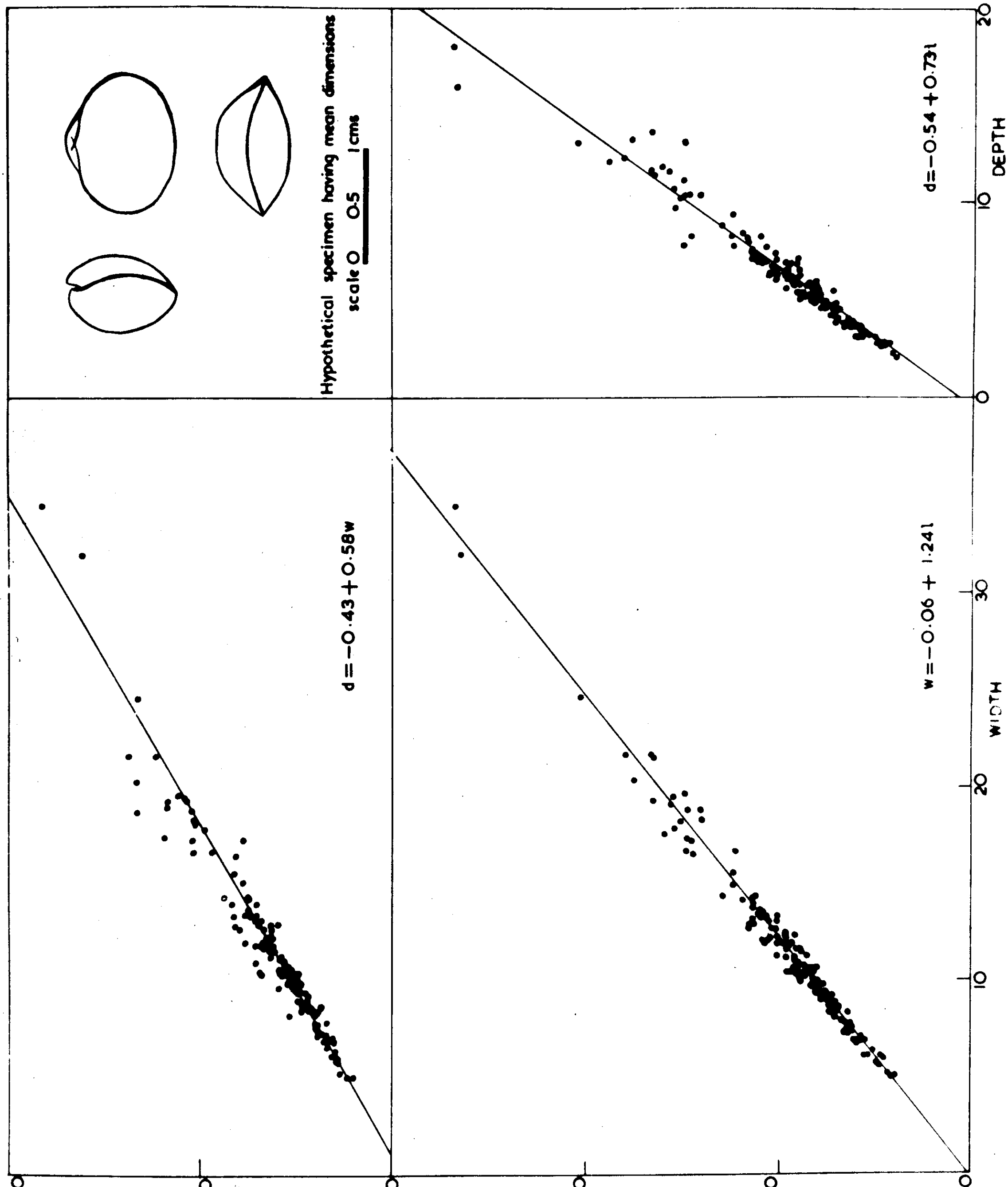
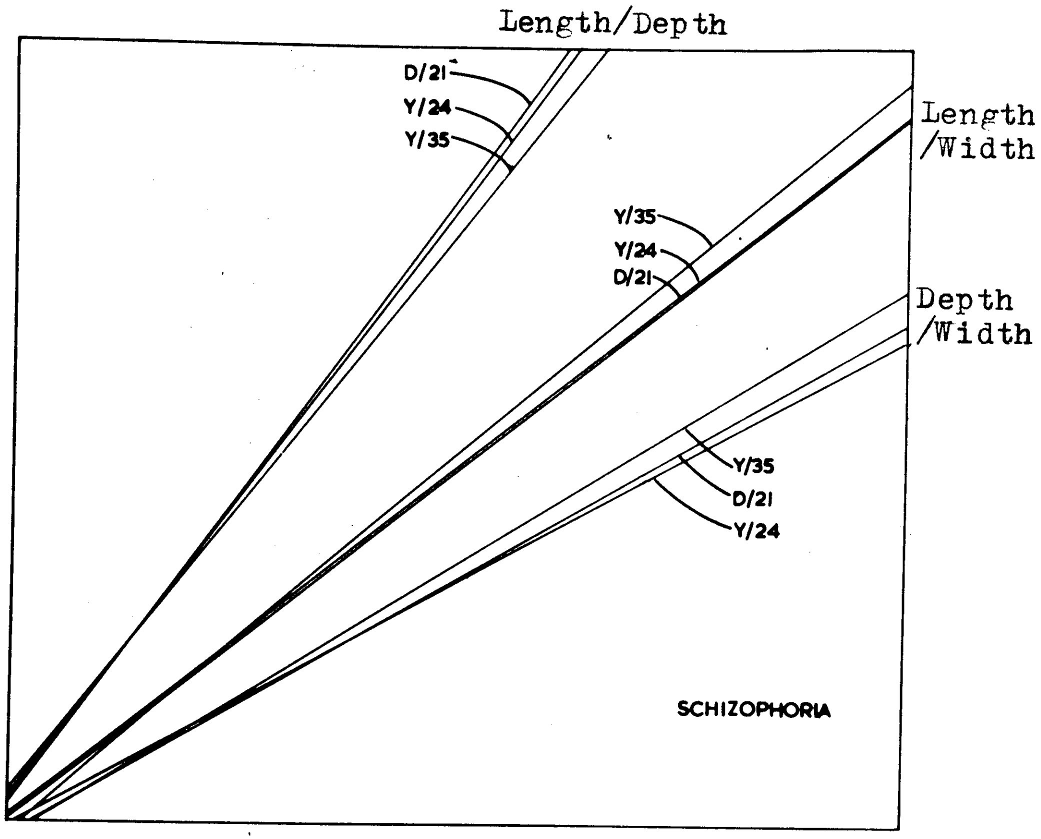


Fig.20.- Scatter diagrams for schizophorias from Locality D/21 Treak Cliff, Derbyshire.



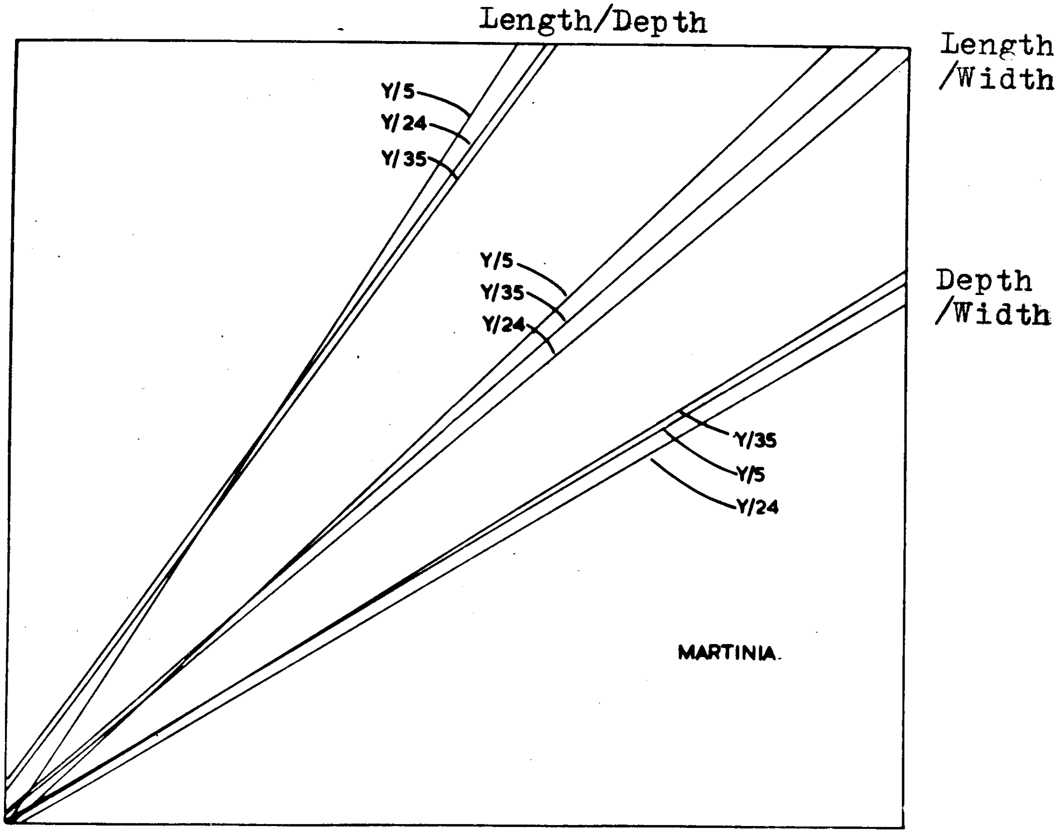


Fig.21.- Comparison of regression lines from figs.15-20.

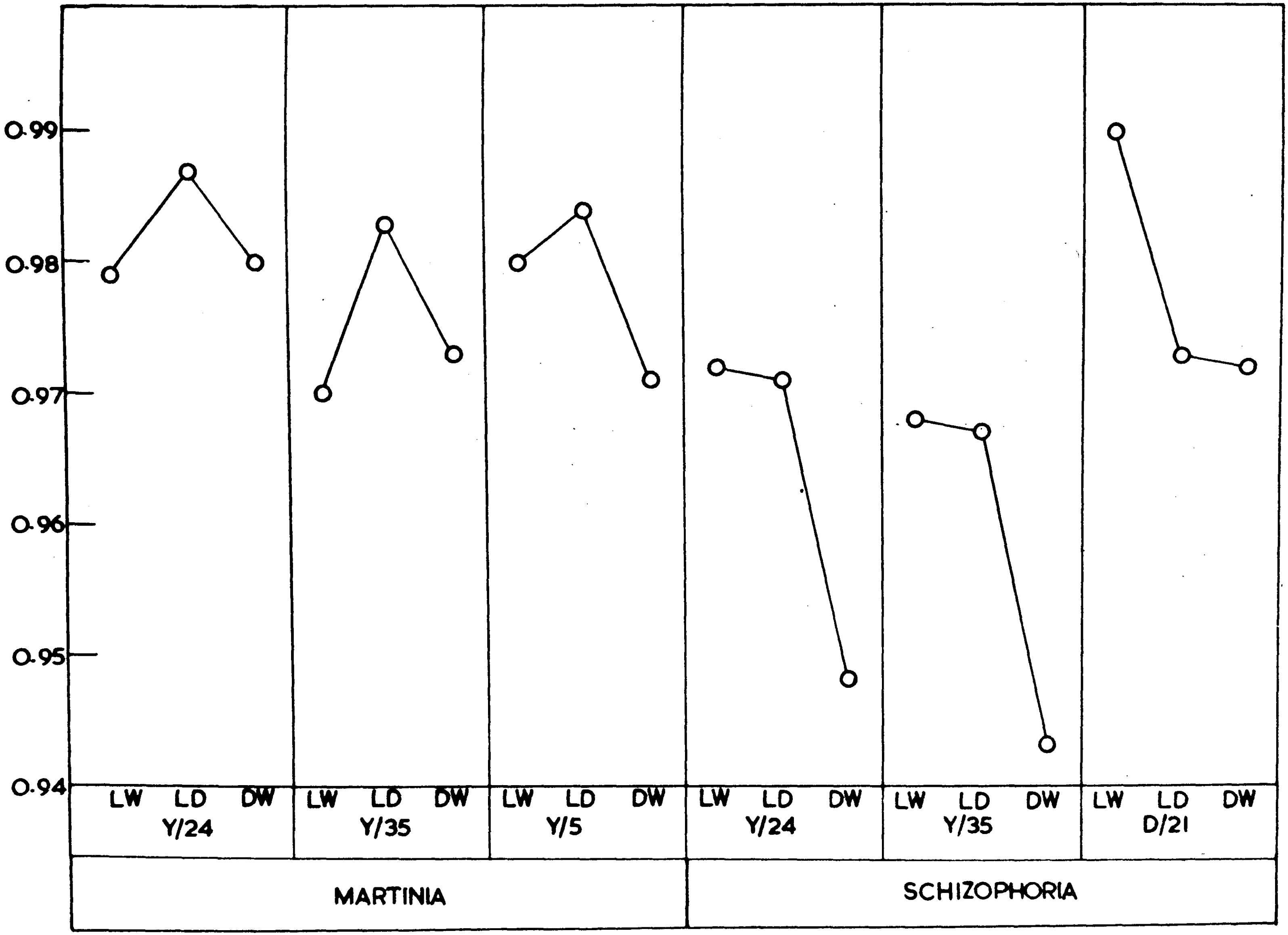


Fig.22.- Correlation coefficients for the samples represented in figs.15-20.

Partial Regression.

The three variables length, width, and depth may be treated simultaneously by the use of the partial regression equation:

$$(l - \bar{l}) = a(w - \bar{w}) + b(d - \bar{d})$$

where l, w, and d represent the mean values of the three principal dimensions.

The equations derived from this serve to emphasise the similarities already indicated, and further comment is unnecessary. The equations for the samples of Martinia are:

$$\text{Loc.Y/5} \quad l = 0.42w + 0.83\,d - 0.89$$

$$\text{Y/24} \quad l = 0.25w + 0.98\,d + 1.24$$

$$\text{Y/35} \quad l = 0.22w + 0.98\,d + 1.57$$

The similarity between localities Y/24 and Y/35 is further indicated by the equations for the samples of Schizophoria:

$$\text{Loc.Y/24} \quad l = 0.39w + 0.65\,d + 0.76$$

$$\text{Y/35} \quad l = 0.41w + 0.62\,d + 0.80$$

The graphical expression of these equations as partial regression planes is given in fig.23.

F-Test and Analysis of Variance.

Comparison between frequency distributions may be made by inspection of mean or modal values, or of range, or of standard deviation, but each of these treat only a part of the results. It is better to conduct analysis of variance tests which treat the whole of the graphed data. Such a comparison is really a detailed investigation of such small

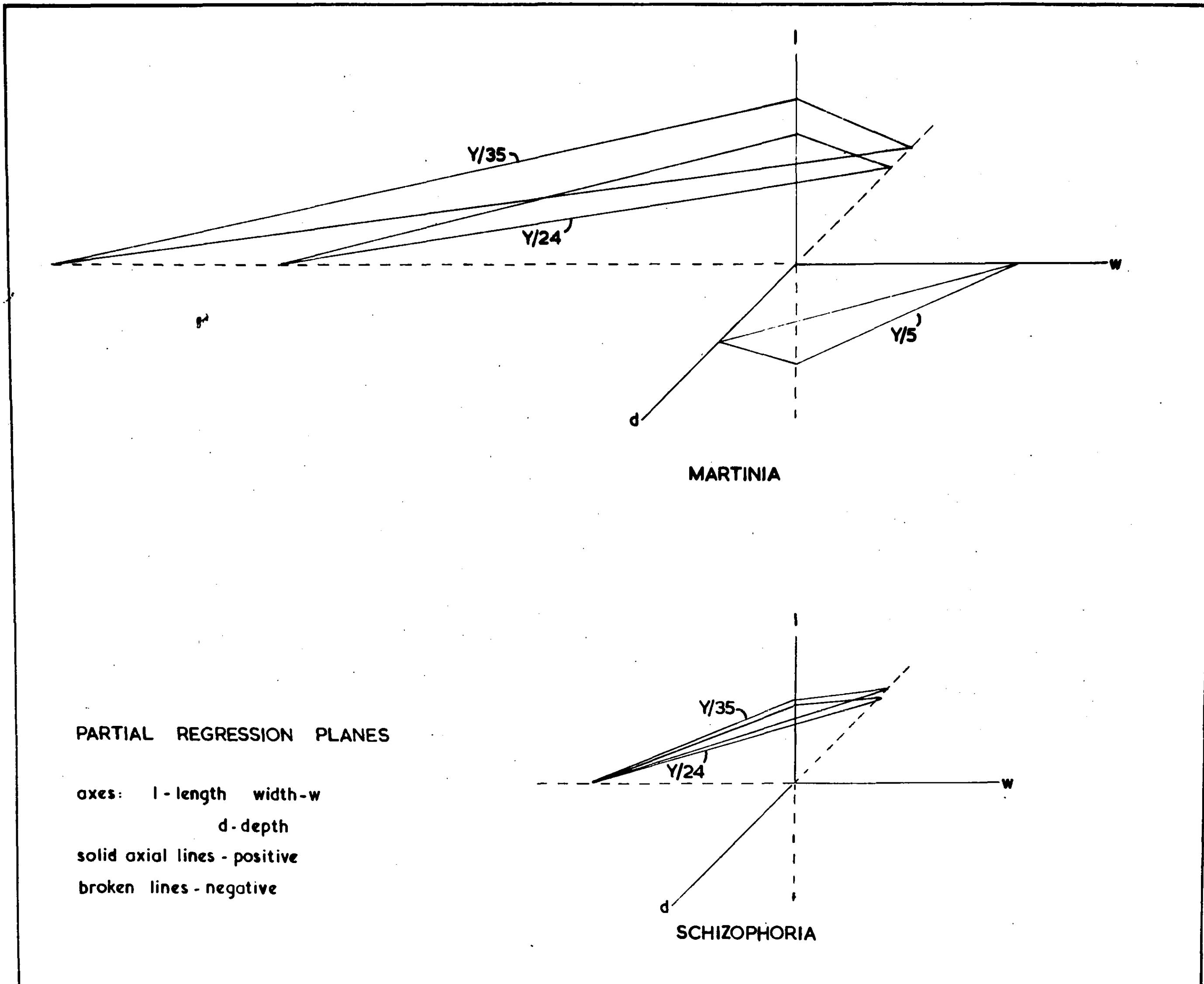


Fig.23.- Partial regression planes for certain of the samples represented in figs.15-20.

differences as do exist between the bounding lines which may be drawn to include all points plotted on the regression graphs. The higher the correlation between length and width, the smaller the range when width/length p.c. is plotted as a frequency distribution. Again width/length is treated in the case of Martinia and depth/length in the case of Schizophoria.

Corrections have been made to one sample of Martinia (that from Locality Y/5) and all but one sample of Schizophoria (that of Locality D/21). The corrections are made by omission from the frequency distributions of those end members which cause departures from linearity in the graphs on the probability scale, and therefore cause slight heterogeneity in the samples. Whereas analysis of the polymodal frequency distributions resulting from their inclusion is impossible from the data present (cf. Jentys - Szaferowa 1938), an approach to isolating the components of the distribution may be effected, as Harding (1949) indicates, using the probability scale.

The mean, standard deviation, number of specimens per sample, and standard error of the mean for each sample is shown (Table V) and this should be compared with the original values of these parameters (Table I) prior to correction.

The method of analysis used is shown in one example (Table VI). The results are summarised in tabular form (Tables VII and VIII).

Conclusions from F-tests on samples of Martinia. Inspection of table VI indicates the degree of difference existing between pairs of samples of Martinia from the localities specified. In certain cases the samples are so similar to one another that the variation within them exceeds that between them. This is indicated by the mean square within groups (the error mean square) exceeding that between groups. Where such occurs the figures for the F-values are not quoted but are replaced by a pair of asterisks.

Slightly greater but still insignificant differences exist between three other sample comparisons. This is indicated by the F-value not exceeding the 5% significance level.

The remaining cases all show a significant value of F. In every case the sample from Locality Y/24 is involved.

In general then, it is shown that a striking similarity exists in some samples derived from geographically widely separated areas while the sample from Locality Y/24 shows significant differences from localities very close to it. The importance of this anomalous sample is discussed after further statistical analysis. Again in order to treat as large samples as possible the grouping of material into size classes has been ignored, but this seems justified in view of the very closely comparable range of size shown by each sample, with the exception of that from Locality Y/5.

Conclusions from F-tests on samples of Schizophoria. In four sample comparisons, an extremely high degree of similarity is indicated by the mean square within groups exceeding that between groups. An insignificant difference exists between the samples from Localities D/21 and Y/39. In three sample comparisons, however, a very high value of F results. In each case the sample from Locality Y/34 is involved. The anomalous natureof this sample also receives further attention below.

In general, the high degree of similarity between samples substantiates that shown in the case of Martinia, and this is of especial importance since the martinias and schizophorias are drawn from the same blocks of limestone. Since this is the case, a difference might have been expected in the schizophorias from Y/24 and other areas, yet this does not occur. A fuller consideration is deferred to the general conclusions from statistical analysis.

Discriminatory Analysis.

For a better picture of the interaction of the three variables length, width, and depth it is obviously desirable to treat all three simultaneously. Normal methods of multivariate analysis, however, such as multiple regression, require that some variable shall be dependent and some other causal. The comparison may be made with univariate analysis where in normal regression the same requirements should be met.

TABLE V

MARTINIA. 100 W/L. (corrected as for F test)

	s	$\bar{x}$	n	s / $\sqrt{n}$.
Loc. Y/5.	9.54	106.020	51	1.336
Y/24.	8.68	114.364	77	0.989
Y/35.	9.74	107.849	152	0.790
Y/39.	11.31	109.758	124	1.016
D/21.	8.48	105.521	71	1.006

SCHIZOPHORIA. 100 D/L. (corrected as for F test)

	s	$\bar{x}$	n	s / $\sqrt{n}$.
Loc. Y/24.	3.48	66.102	49	0.497
Y/34.	4.76	50.899	79	0.536
Y/35.	3.68	66.543	35	0.622
Y/39.	4.64	66.868	68	0.563
D/21.	5.71	65.642	137	0.488

TABLES VI, VII

ANALYSIS OF VARIANCE.

Method used for comparison of two samples, with respect to ratio 100 Width / Length.

Ratio represented by X. In calculating sum of squares for groups,

$$\sum G_1 + \sum G_2 = \sum X$$

Total sum of squares given by:

$$\sum X^2 - (\sum X)^2 / n$$

Groups sum of squares given by:

$$(\sum G_1)^2 / n_1 + (\sum G_2)^2 / n_2 - (\sum X)^2 / n$$

In comparison of 100 Width/Length of 152 Martinia from locality Y/35 and 77 from locality Y/24:

Total sum of squares = 22,207.

Groups sum of squares = 2,169.

Analysis of variance:

Source of variation.	Degrees of freedom.	Sum of squares.	Mean squares.
Total.	228	22,207	
Groups.	1	2,169	2,169
Error.	227	20,038	88.273

$F = 2{,}169/88.273 = 24.57$ $F_{.05} = 3.89$

$F_{.05}$ is the five per cent. significance level which is exceeded in the above example indicating a significant difference between the samples.

The remainder of the results are summarised in tabular fashion, in the following pages.

TABLE VI.

ANALYSIS OF VARIANCE.

100 Width / Length. MARTINIA.

SUMMARY OF F-VALUES.

	Y/24.	Y/35.	Y/37.	Y/39.	D/15.	D/21.
Y/5.	26.20 3.92	1.35 3.89				**
Y/24.		24.57 3.89				39.21 3.91
Y/35.				**		2.98 3.89
Y/37.				3.19 3.91		
Y/39.					**	
D/15.						

Explanation: Upper row of figures indicates F-values for the pairs of samples analysed. Beneath them is recorded the 5% significance level for the number of individuals in the two samples. Where a greater mean square exists within groups compared with that between groups, it is indicated thus: **

TABLE VII.

ANALYSIS OF VARIANCE.

100 Depth / Length. SCHIZOPHORIA.

SUMMARY OF F-VALUES.

	Y/34.	Y/35.	Y/39.	D/21.
Y/24.	375.32 3.92	**	**	**
Y/34.			421.35 3.91	375.70 3.89
Y/35.			**	
Y/39.				2.38 3.89

Explanation as for Table VI.

A method which treats a series of variables as all having equal status is that used by Barnard (1935) and Fisher (1936). The main feature of this Discriminatory Analysis is that it weights the differences that one wishes to emphasise; the differences between samples, rather than the heterogeneity within them. In the words of Kendall (1946) its function is "... to minimise the sum of squares within species, and for a constant total to maximise the sum between species."

The "species" are here replaced by samples of conspecific individuals.

Two comparisons have been made using this method. In the first 79 specimens of _Martinia_ from Locality Y/24 and 155 from Locality Y/35 are compared. In the second 58 specimens of _Schizophoria_ from Locality Y/24 are compared with 137 from Locality D/21. The method used in these examples (Table VIII), followed by the summary of results for each (Tables IX and X), is given in the succeeding pages.

The results of these two selected examples indicate that there is no linear function which can differentiate between the samples compared. In each case the value of F is well below the five per cent significance level. The discriminatory analysis of the _Martinia_ samples is also carried out on the same material as for the univariate analysis, and the correspondence of the results is clear.

It may reasonably be assumed, then, that the various

TABLES VIII, IX

DISCRIMINATORY ANALYSIS.

The method used is as follows:

The difference between the mean values for length ($\bar{l}$) width ($\bar{w}$), and depth ($\bar{d}$) is d_1, d_2, and d_3 respectively.

The sums of the values of length for the two samples is pooled , and width and depth treated similarly. The variances and covariances derived from these pooled totals are expressed as a matrix:

$$\begin{bmatrix} \text{var } l & \text{cov } lw & \text{cov } ld \\ \text{cov } lw & \text{var } w & \text{cov } wd \\ \text{cov } ld & \text{cov } wd & \text{var } d \end{bmatrix}$$

The matrix is inverted:

$$\begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{12} & a_{22} & a_{23} \\ a_{13} & a_{23} & a_{33} \end{bmatrix} \qquad \begin{bmatrix} a^{11} & a^{12} & a^{13} \\ a^{12} & a^{22} & a^{23} \\ a^{13} & a^{23} & a^{33} \end{bmatrix}$$

where

$$a^{11} = a_{22} \cdot a_{33} - a_{23} \cdot a_{23}$$

$$a^{12} = a_{13} \cdot a_{23} - a_{12} \cdot a_{33}$$

The coefficients of the required linear equation;

$$X = \lambda^1 l + \lambda^2 w + \lambda^3 d$$ are given

$$\lambda^1 = d_1 a^{11} + d_2 a^{12} + d_3 a^{13}$$

and etc. symmetrically.

TABLE VIII.

Discriminatory Analysis.

MARTINIA. Localities Y/24 and Y/35.

	$\bar{l}$	$\bar{w}$	$\bar{d}$	n
Y/24	14.551	16.696	9.375	79
Y/35	14.583	15.721	9.674	155

d_1	d_2	d_3
0.032	-0.975	0.299

var (l)	var (w)	var (d)
29.5310	40.2690	15.9891

cov (lw)	cov (ld)	cov (wd)
33.4612	21.3739	24.5793

Matrix:

$$\begin{bmatrix} 29.5310 & 33.4612 & 21.3739 \\ & 40.2690 & 24.5793 \\ & & 15.9891 \end{bmatrix}$$

Inverted matrix:

$$\begin{bmatrix} 39.7231 & -9.6590 & -38.2527 \\ & 15.3305 & -10.6550 \\ & & 69.5319 \end{bmatrix}$$

$\lambda 1 = -0.7480$ $\lambda 2 = -18.4421$ $\lambda 3 = 9.1773$

$X_{24} = -232.7561$ $X_{35} = -212.0551$

Analysis of variance:

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Total	233	7368.41	
Between localities	3	176.67	58.890
Error	230	7191.74	31.268

$F = 58.890 / 31.268 = 1.88$ $F_{.05} = 2.65$

TABLE IX.

SCHIZOPHORIA. Localities Y/24 and D/21.

	$\bar{l}$	$\bar{w}$	$\bar{d}$	n
Y/24	9.793	12.219	6.609	58
D/21	9.709	11.991	6.504	137

d_1	d_2	d_3
0.084	0.228	0.105

var (l)	var (w)	var (d)
12.503	19.983	6.978

cov (lw)	cov (ld)	cov (dw)
15.602	9.085	11.443

Matrix:

$$\begin{bmatrix} 12.503 & 15.602 & 9.085 \\ & 19.983 & 11.443 \\ & & 6.978 \end{bmatrix}$$

Inverted matrix:

$$\begin{bmatrix} 8.499 & -4.911 & -3.012 \\ & 4.709 & -1.328 \\ & & 6.425 \end{bmatrix}$$

$\lambda 1 = -0.722$ $\lambda 2 = 0.522$ $\lambda 3 = 0.119$

$X_{Y/24} = 0.094$ $X_{D/21} = 0.023$

Analysis of Variance:

Source of variation.	Degrees of freedom.	Sum of squares.	Mean square.
Total	194	0.139	
Between localities	3	0.00008	0.00003
Error	194	0.139	0.00073

As the mean square between localities is less then the error mean square, the difference between samples is insignificant.

types of univariate analysis used are reliable indicators of degrees of difference between samples.

Significant difference in the ratio of width to length has been indicated (analysis of variance of ratio 100W/L *Martinia*, Locality Y/24). However, the discriminatory analysis applies to a linear function:

$$X = \lambda_1 l + \lambda_2 w + \lambda_3 d$$

and the ratio 100W/L cannot be strictly compared.

The general conclusion from the discriminatory analysis is that no significant difference exists between the samples compared. Were the sample of *Schizophoria* from Locality Y/34 to be treated in this way it is almost certain that the significance level would be exceeded.

IX. CONCLUSIONS FROM STATISTICAL ANALYSIS.

The general similarity graphically illustrated by familiar statistical techniques is supported by the results derived from detailed comparison in a series of F-tests. This similarity is best shown by use of discriminatory analysis, but the ease with which the F-test and analysis of variance may be applied has led to its use over a greater number of samples.

Two main deviations from the all-over similarity between demes are brought out. The schizophorias of Locality Y/34 differ significantly in size and in proportion. The martinias of Locality Y/24 differ significantly only in proportion. Silvester-Bradley (1951) suggests that samples showing a deviation in their distribution about the mean of

$$\pm\ 2\ s_m \quad \text{where } s_m = s/\sqrt{n}$$

should be considered as differing at a sub-specific level. Parkinson (1952 ex.ms.) replaces the constant 2 by 2.6, otherwise his definition is the same. If the statistical limits of a sub-species formulated on theoretical grounds be accepted, then it may be seen how the martinias of Locality Y/24 fit this arbitrary limitation. From the values shown (Table IV) the following details may be calculated:

1. Locality Y/34 <u>Schizophoria</u>. 100 d/l.

$$\text{mean} + 2\ s_m = 51.970$$

$$\text{mean} + 2.6\ s_m = 52.292$$

The nearest mean value, namely that of the sample from Locality D/21 gives:

$$\text{mean} - 2\ s_m = 64.666$$

$$\text{mean} - 2.6\ s_m = 64.374$$

Both of these values lie well outside the mean value of all other samples. The much greater size of the schizophorias of Locality Y/34 and their general morphology add weight to this distinction. The schizophorias of Locality Y/34 probably belong to a distinct species.

2. Locality Y/24 Martinia. 100 w/l.

$$\text{mean} - 2\ s_m = 112.386$$

$$\text{mean} - 2.6\ s_m = 111.792$$

The nearest mean value, namely that of the sample from Locality Y/39 gives:

$$\text{mean} + 2\ s_m = 111.789$$

$$\text{mean} + 2.6\ s_m = 112.399$$

The only difference between the martinias of locality Y/24 and those of other localities is one of proportion, and if Parkinson's limitation of the sub-species is accepted then such a genetic difference exists in this case. In this locality, unlike Locality Y/34, both Schizophoria and Martinia are present in the samples. It is therefore possible to determine the presence of differences in the complementary genus.

The schizophorias of Locality Y/24 do not show significant differences when compared with other samples, if exception be made of course of that from Locality Y/34. Therefore, the variation which does occur in the martinias cannot be attributed to environmental modification, which would certainly have had an effect on the apparently more variable schizophorias.

That a difference in age of the deposits is not the cause of this variation is indicated by the same consideration. Such a difference would imply that Schizophoria is the more conservative genus of the two, yet the degree of variation, in ribbing, in inflation, in resupination, and in orientation of the interareas would not support such an implication.

It may be concluded then that the martinias of Locality Y/24 are sub-specifically distinct from those of all other locality samples analysed.

X. SUPPLEMENTARY EVIDENCE ON ENVIRONMENT.

Generic Variation of Assemblages.

The general variation in association of genera in assemblages is not to be taken as being indicative of difference in age or difference of enclosing sediment, though slight changes in environment such as degree of exposure to open sea conditions may be postulated. As is indicated by the diagram (fig.4), a considerable difference does exist in general generic composition of these population samples.

Stephen (1929, 1930) has shown that considerable variation occurs in the Scottish marine lamellibranch faunas of the present day. Variation takes the form of a relative change in quantity of genera over very short distances. He notes (1930) that an identical shell "sand" substratum in two localities on Tiree supports greatly differing faunas, the change being due to a difference in the exposure to Atlantic storms. Other factors shown to cause this type of variation include changes in the quantity of spat fall from year to year.

MacLennan (1945) finds that polymodal frequency distributions result from measurement of a particular 'population' of non-marine lamellibranchs. This is inferred as being due to year to year variations in favourability of conditions for metamorphosis, following spat fall. Consequently, different generations show variation in numbers, and this is brought out by a series of modes at different sizes of individual in the frequency polygon.

Thorson (1946) notes that in certain years extremely large spatfalls of individual species, may occur, though in general the number of adults fluctuates only slightly from year to year.

It is to be noted, however, that Thorson referred to marine bottom invertebrates over a large area while Stephen's work was conducted on a purely neritic fauna and differentiated between ecological position. Thus the latter is probably more meaningful for comparison with the reef knoll faunas.

Growth Halts.

Orton (1926) has described the effects of removing individuals of *Cardium edule* from their position of rest and exposing them for a short time to drying conditions. A "disturbance-ring" results and, as his photographs show, such rings exactly resemble the more prominent growth halts on many of the brachiopods from Locality D/21. These rings are very marked in schizophorias from this locality and they occur in martinias in sufficient relief to allow of growth stage determinations. They are also present in the brachythyrids.

These shells must have been exposed repeatedly to slight deterioration of environment though whether changes in salinity, temperature, dessication or food supply are involved, cannot be determined.

Malformed Individuals.

Asymmetrical and malformed specimens of Martinia are not uncommonly found, and indicate some impediment to equal growth. Cooper (1937) makes similar observations and suggests overcrowding during development as the most likely cause. The external morphology of both Schizophoria and Martinia indicates that there are a limited number of ways in which these shells could live. Either the open or partly open delthyrium was functional and they were pedunculate forms, or it was functionless during a part or the whole of the life of the individual, and the shells lay free on the substratum or partially embedded in it. Therefore the malformations may be explained as the result of growth in crowded conditions as Cooper suggests, or they may be attributed to pathological causes. The latter mechanism has been suggested by Reed (1893) to explain the unequal growth in certain specimens of "Spirifer lineata" leading to the development of a sinus in both ventral and dorsal valves. He envisaged parasitism of the mantle as partially inhibiting the normal secretion of shell material.

If Reed is correct, such parasitism would need to be selective, as Schizophoria only rarely exhibits any degree of asymmetrical growth. The suggestion which Cooper gives is perhaps more readily acceptable.

Occasional specimens of Schizophoria show a great development of convexity of the dorsal valve with a corresponding flattening and subordination of the ventral valve. The frequency of occurrence is about once in thirty individuals. Such morphological development may be paralleled in the Strophomenoidea, where certain genera exhibit a plano-convex appearance though resupination and concavo-convex shells are more typical. In the case of the Strophomenids, the constant increasing of convexity or degree of resupination is designed to keep the anterior margin from contamination with mud.

While a similar explanation may be apposite in the case of the schizophorias a true analogy cannot be made. The unusually convex individuals are aberrant forms, not distinct genera. They may therefore be the result of genetic mutation, and without survival value.

Some of the brachythyrids from D/21 show replacement of damaged parts of the shell. A thickened shell layer is deposited over such parts leaving a decided interruption in the level of the shell surface, but not disturbing the continuity of direction and co-linearity of the costae across the regenerated shell.

Summarising, it appears that the conditions operative during the deposition of the Treak Cliff reef-limestones showed a greater degree of disturbance of tranquil conditions than occurred in the Cracoe reef-belt.

Variation in Lithology.

In hand specimen the limestones are generally fine-grained and light brown to light grey in colour. Patches of tufa stand out on the weathered surfaces particularly in some of the Elbolton localities. Little differentiation is possible without recourse to thin section.

Thin Section Analysis. Thin section examination discloses no striking differences between the reef limestones of Yorkshire and Derbyshire. They are mainly fine-grained and largely recrystallised. Patches of calcite mud are very common, and true grain limestones (Wood 1941) occur, the grains consisting of organic detritus or fragments of calcite mud and being usually rounded or sub-angular. Occasionally, there is a gradation into quite coarse shell-fragment limestones with a matrix of recrystallised calcite.

A common occurrence is the aggregation of minute particles probably of calcite dust into circular areas (spherical in three dimensions) of about 0.3 mm. to 0.4 mm. diameter. They may be scattered about the section but usually are concentrated into fairly discrete areas. They closely resemble the description of "algal-dust" given by Wood (1941). This is supported by the occurrence of algae throughout many of the sections. Slightly larger elliptical patches of similar appearance in detail under high-power (x 400) may correspond to the "pellet limestone" described by Black (Hatch and Wells 1938, p.169).

No true oolite grains have been encountered in over one hundred micro-sections.

Recrystallisation occurs in practically all cases. Occasionally it is complete, at other times it is selective so that large plates are present usually clouded with inclusions of algal-dust. Whether true argillaceous material is present is doubtful, though many of the darker masses may have a small clay fraction. Bands of tufa are occasionally present. They are characterised by prominent plates of calcite disposed at right angles to the organic material usually enveloped.

The shell fragments often present are supplemented by corals rarely and crinoid plates frequently. The latter may sometimes give rise to a true crinoid breccia. Recrystallisation often tends to render the crinoid plates shadowy and irregular in outline. Algae and bryozoa make up a considerable amount of the organic material, and foraminifera are locally very abundant. Some ostracods occur.

Most sections show development of secondary silica. This is indicated by the presence of well-formed grains of quartz. That they are actually secondary is indicated by the sharp crystal faces and the good hexagonal and prismatic sections present. Furthermore, inclusions often make up a central core, or are disposed zonally, parallel to the crystal faces. In some cases the grains coalesce and patches of silicified limestone occur.

Dolomitisation has not been observed.

In some cases the twin lamellae of the calcite are curved, indicative of post-consolidation movement.

Principal localities. Certain of the localities to the samples of which particular attention was directed in the statistical analysis may now be compared.

The limestone of Locality Y/5 varies from a grain limestone of small shell fragments to one of finer grain with patches of calcite mud. Algal dust, bryozoa fronds, and crinoid plates are present. Recrystallisation apart, there is no evidence of secondary change.

Thin sections from Locality Y/24 show a very fine grain limestone containing certain discrete areas of material similar to the pellets mentioned above.

Locality Y/35 shows limestone which is largely recrystallised and tufa often invests the brachiopod shells. True grain limestone has not been observed and there is little organic material apart from the macro fossils, although algae and bryozoa are not uncommon. Silicification occurs in the form of finely disseminated but distinct grains of quartz.

The limestone of Locality Y/39 is similar and is almost completely recrystallised. Some areas may be argillaceous, though more probably they represent dense aggregations of minute calcite needles.

The Derbyshire localities do not differ consistently. The limestone of Locality D/15 is recrystallised, laced with fronds of bryozoa and spotted with indeterminate patches of calcite dust.

Greater variability occurs in the sections taken from the Treak Cliff Locality D/21. Patches of calcite mud, grain limestone, and shell fragment limestone on a coarse scale are all present. Areas of pellet limestone may be developed and algal dust is scattered throughout. Recrystallisation is usual, and bands of tufa are often found, yet certain areas occur which are completely unaffected by recrystallisation and their appearance suggests an argillaceous composition. Foraminifera are quite plentiful in some sections. Curved calcite twin lamellae occur and incipient silicification is present throughout.

Other localities. The remaining localities show a greater amount of grain limestone and a much more abundant micro-fauna.

The Butterhaw Knoll samples all of which are as near as can be ascertained, from the same bed, are especially rich in bryozoan fragments.

A section from Carden Hill shows a very fine grain limestone with small foraminifera plentifully developed. A section from Locality Y/28 (Stebden) has a practically identical aspect. It is to be noted that whenever a fine grained limestone occurs the foraminifera are small. Whether these protozoans are pelagic or benthonic does not alter the expectation of finding them exhibiting variation in size with complete disregard for the texture of the matrix. It is further evidence that sorting has occurred.

The Thorpe Kail Hill localities show a predominance of grain limestone which are fairly rich in foraminifera. Yet from these localities brachiopods have not been obtained in quantity. The reason appears to be not so much a primary lack of association between the two, but a greater ease of extraction of macro-fossils from the recrystallised limestones, and a degree of intractibility in the tough grain limestones which renders mechanical extraction difficult.

Beautiful grain limestones of even texture are present at Byra Bank, and both these and limestones of extremely fine grain occur at Hartlington Kail.

The limestones of the Malham knolls exhibit similar textural features.

The auxiliary Derbyshire localities provide complementary evidence. Grain limestone with foraminifera is plentiful in other localities on Treak Cliff. Many of the sections from the Derbyshire reef-limestones are greatly altered by secondary processes and silicification reaches greater proportions with the selective occupying of areas of algal dust by coalescing quartz grains.

The above considerations indicate that between localities there is no distinction to be drawn which would give evidence of substantial environmental differences. A type of lithology developed in a particular locality on Elbolton may differ from that of a nearby section yet be repeated with fair exactitude in a sample taken from Treak Cliff in Derbyshire. The only definite conclusion which may be drawn is that a very fine grain limestone present in one locality may pass into a medium grained limestone within a very short distance. Often the two textures are present in the same thin section, grading imperceptibly into one another. The greatest number of brachiopods have been obtained from the very fine grained members, which have usually undergone a high degree of recrystallisation. Large shell fragments do not occur in the grain limestones, probably because of sorting of comminuted material.

XI. THE AGE OF THE DEPOSITS.

The most recent mapping of the knolls of the Cracoe area of Yorkshire is that of Bond (1950). He assigns an age of Middle to Upper D_1 to the highly fossiliferous limestones from which most of the present collecting has been done.

Parkinson (1947) has indicated a B_2 age for the Treak Cliff area which includes the localities studied in the present work. The equivalence accepted between B_2 and D_1 would indicate contemporaneity between the reef deposits of the two areas.

Shirley (1940) describes the unconformity at Pindale to show that the reef limestones overlie horizons up to at least part of D_2. On the other hand, he mentions that stacks of D_1 limestone protrude through the mantling reef on Treak Cliff. There is no indication that this occurs in Locality D/21. Shirley also holds that <u>Cyrtina septosa</u>, high D_1 indicators which occur along with B_2 goniatites, are actually derived fossils. If the same reasoning be extended to the Cracoe knolls then there is no opposition in Shirley's work to equating the reef limestone of the two areas in age. It is simply that the equation would be effected at a higher stratigraphical level in the case of Shirley's mapping.

The close similarity demonstrated statistically between species-assemblages in the two areas in the present work argues the similarity in age of the reef-limestones of the two areas.

This may be contended with greater assurance in view of the recent work of Parkinson (1952 MS.). He has analysed samples of <u>Schizophoria</u> from horizons from C_2 to D age. In the ratios indicated, he gives the following degree of variation:

	C_2	D
Mean D/W	0.4506	0.5582
D/L	0.5721	0.6468
L/W	0.7868	0.8261

where D, W, and L represent depth, width, and length respectively.

Corresponding ratios may be given for the schizophorias considered in the present work:

	Y/35 (n=39)	Y/24 (n=58)	D/21 (n=137)
Mean D/W	0.5676	0.5409	0.5424
D/L	0.6883	0.6749	0.6699
L/W	0.8247	0.8015	0.8097

Two important points may be made. Parkinson has shown that a demonstrable degree of variation in proportion does occur, which indicates that the similarity shown therein, between unitary demes, is meaningful. Secondly, the correspondence of the figures from all three localities to those of Parkinson for <u>Schizophoria resupinata</u> from D horizons is in broad agreement with the contention that the reef-limestones of Craven and Castleton do in fact belong to the Dibunophyllum zone. The general similarity of the figures to those of Parkinson overrides the determinations for L/W for Y/24 and D/21 which are not indicative either way.

The generic variation in the aspect of the brachiopod faunas is not to be taken as indicating age variation as Stephen has shown the degree of variation in quantity of particular species which may be found on present-day shores.

It may be asserted then that the reef-limestones of the Cracoe area of Yorkshire, and the Castleton area of Derbyshire, are contemporaneous, in so far as may be indicated by the above considerations.

XII SUMMARY AND CONCLUSIONS

Previous studies such as those of Willard (1930) and Parkinson (1952 abstract) have shown that changes in shell shape of certain brachiopod genera can be demonstrated at successive horizons.

In the present work, changes in shell shape have been investigated in individuals belonging to samples from different localities. Homogeneity exists within the samples, as is shown by the normality of the frequency distribution curves. Continuous variation may be demonstrated throughout series embracing quite different shapes of shell.

To ensure that the samples represent approximately contemporary populations, the collecting has been closely localised, some samples being the products of single blocks of limestone. In some cases the shells of a sample are covered by an encrusting layer of bryozoa,adding weight to the contention that they are virtually of the same age.

The major part of the work is concerned with the differences exhibited between samples. If the assumption is made that the samples are in fact derived from deposits of the same age, then the variation they exhibit will be due entirely to genetic or to environmental causes. A certain part of the variation is ascribed to each of these, and as the variation which remains is statistically insignificant the assumption of contemporaneity is justified.

Thus the reef limestones of the Craven district of Yorkshire may be equated approximately in age to those of the Castleton area of Derbyshire.

Parkinson (Ms 1952) gives certain statistical data for Schizophoria resupinata which is closely paralleled when applied to the schizophorias from the samples under consideration.

His statistics are extended in the present work which is based entirely on closely localised samples rather than including uncertainly localised aggregates from museum collections. Further the application of the same statistical techniques to species-assemblages from two quite different groups of brachiopods has made distinction possible between the variation due to genetical constitution and that due to environment. The way in which statistical comparison between samples of Martinia aff. glabra agrees with similar comparisons between samples of Schizophoria resupinata affirms the assertion that the limestones from which they have been derived are similar in age.

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