THE SIGNIFICANCE OF ORIENTED
CORAL SECTIONS

Thesis for the Degree of M. S.
MICHIGAN STATE COLLEGE

Warren Edward Grabau
1950

This is to certify that the

thesis entitled

"The Significance of Oriented Coral Sections"

presented by

Warren Edward Grabau

has been accepted towards fulfillment of the requirements for

Master's degree in Geology

William A. Kelly
Major professor

Date May 25, 1950

O-169

THE SIGNIFICANCE OF ORIENTED CORAL SECTIONS

by Warren Edward Grabau

A THESIS

Submitted to the Graduate School of Michigan
State College of Agriculture and Applied
Science in partial fulfillment of the
requirements of the degree of

MASTER OF SCIENCE

Department of Geology
and Geography

1950

THESIS

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ACKNOWLEDGMENTS

I am indebted to Dr. William A Kelly, of Michigan State College, for his considerable assistance and cooperation. To Arthur Slaughter I am obligated, because of his enthusiastic collection of samples from areas which I was not able to reach. I am grateful to Dr. B. M. Stewart, of the Mathematics Department, for his aid in the solution of the nomogram included in this paper. Mr. E. J. Wade is largely responsible for the photographic material included.

INTRUDUCTION AND PURPOSE

In the examination of fossil animals, paleontologists are forced to rely on only a portion of the evidence available to biologists who study modern faunas. Specific determinations of contemporary animals are made on the basis of both soft and hard parts. Because paleontologists are restricted to skeletal characteristics alone, it is inevitable that their determinations will not have the precise values possessed by identifications made from soft parts as well as skeletons. This is especially true in those cases where skeletons exhibit convergent, or parallel features, presenting similiar characteristics in quite different groups. Closely allied species may have nearly or entirely identical skeletons, and paleontologists cannot be expected to identify them as individuals.

Modern biologists, who work with the living fauna of the planet, are accustomed to the notion that wide variation in morphological characteristics is possible within a given species. For instance, fishes of the same species not infrequently have different numbers of vertebral segments. Corals exhibit quite different corallum shapes within the same species, and within very narrow areal limits.

These differences, in most cases, can be correlated with environmental factors (Vaughan, 1917).

The question was, how does one detect the difference between a variation within a species and a variation due to different species? The most obvious approach was to collect as many specimens as possible, and examine them for overlapping characteristics. In theory, there should be a consistent difference of some nature between two species. But if the forms are only variations with species, there ought to be a fairly consistent overlap of characteristics, such that specimens would grade imperceptibly into each other. A plot of variation limits should then be possible, and any breaks in the sequence could then be interpreted as specific breaks (Simpson, 1937).

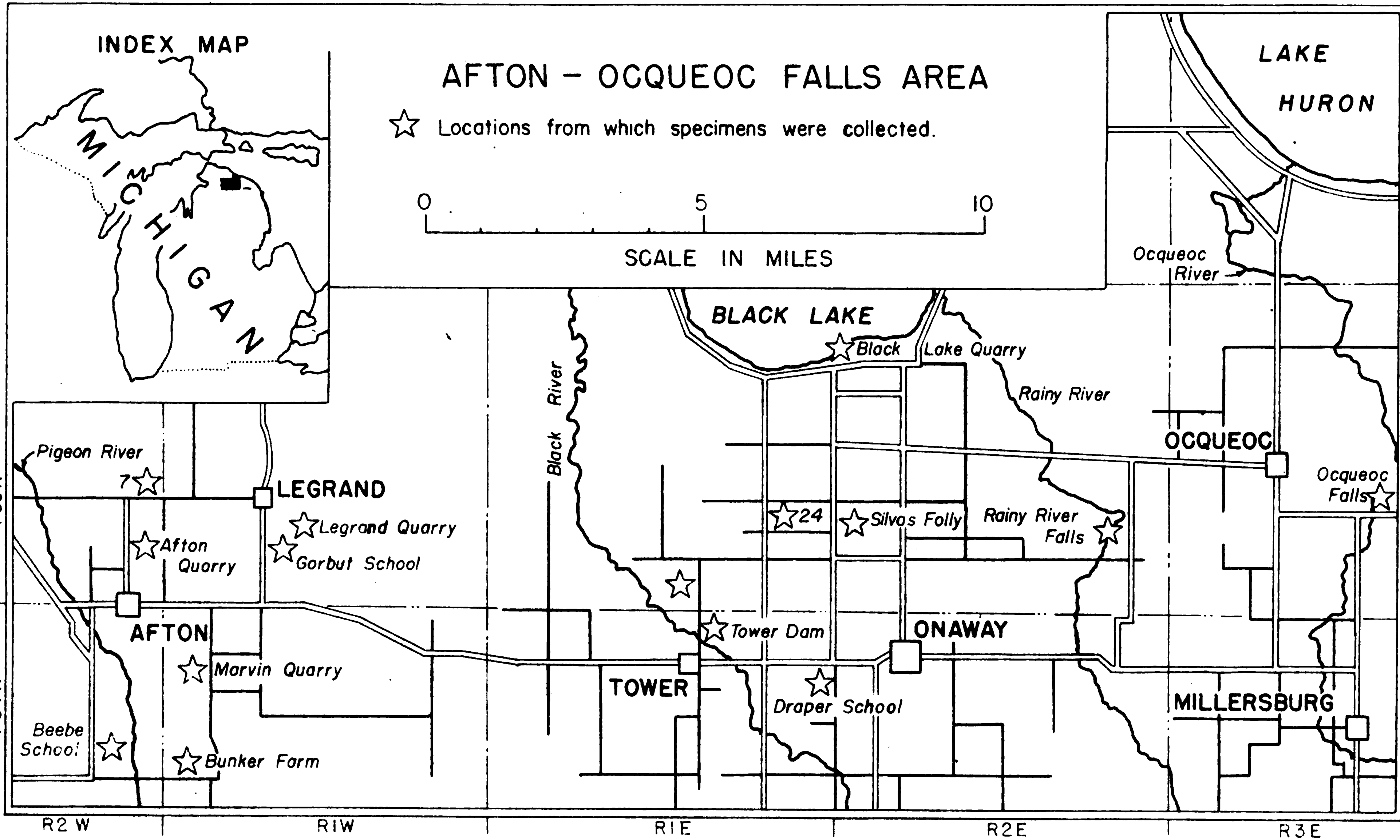
As a complicating factor, the theory suggested that some variation would be found within a single corallum, because the environment would not be the same over the entire colony. For example, food supplies might not be uniform because one side of the colony would be in a more advantageous position with respect to the food-bearing currents. In the domal colonies, some corallites at the periphery would be bothered more by mud and absence of light than would those near the apex. These considerations made it necessary to examine each corallite of every colony individually.

To insure that no portion of the coral skeleton was neglected, a system of oriented sections was designed. A series of four sections was found to be most useful. Study with the oriented sections revealed that the structure of the coral animal is exceedingly complex. Gradually this line of endeavor became a technique for the study of <u>Hexagonaria</u>, and it is this technique which furnishes the body of this paper.

The descriptive terminology used in this paper is that used in Sanford's (1939) excellent summary of the families of tetracorals. Where new or modified terms are used, they are defined in the text, or illustrated, or both.

STRATIGRAPHY

The fossil corals used in this study were collected from outcrops of the Traverse group in the north-central part of the lower peninsula of Michigan. The locations of the various outcrops are noted on the accompanying map of portions of Cheboygan and Presque Isle counties. Most of the specimens were collected during the summer of 1949 by the writer, and by members of the student body of Michigan State College while on a field trip to the area. Additional material belonging to the collection of Henry Faul was later included as better techniques for the interpretation of random sections were developed.


AFTON – OCQUEOC FALLS AREA
Locations from which specimens were collected.
0
5
10
SCALE IN MILES
INDEX MAP
MICHIGAN
LAKE HURON
Ocqueoc River
BLACK LAKE
Black Lake Quarry
Rainy River
Black River
OCQUEOC
Ocqueoc Falls
Pigeon River
7
LEGRAND
Legrand Quarry
Gorbut School
Afton Quarry
AFTON
Marvin Quarry
Beebe School
Bunker Farm
24
Silvas Folly
Rainy River Falls
Tower Dam
TOWER
ONAWAY
Draper School
MILLERSBURG
T 36N
T 35N
T 34N
R2 W
R1W
R1E
R2E
R3E

INDEX TO LOCATION MAP

Location	Specimen number	Location number	Formation
Afton Quarry	200	5	Gravel Point
" "	100	5	Gravel Point
" "	13-1**	5	Gravel Point
" "	14-1	5	Gravel Point
Legrand Quarry	400	9	Gravel Point
" "	450	9	Gravel Point
Draper School	21-1	28	Gravel point
Bunker Farm	7-1	14	Gravel Point
Gorbut School	11-1	9	Gravel Point
Beebe School	2-2	1	Gravel Point
" "	2-1	1	Gravel Point
Afton Quarry	25	5	Koehler
" "	30	5	Koehler
" "	35	5	Koehler
Silva's Folly	15	12	Genshaw
Tower Dam	18-1	21	Genshaw
" "	18-2	21	Genshaw
" "	18-4	21	Genshaw
Rainy River Falls	29-1	13*	Genshaw
unknown location	24-1		Genshaw
unknown location	23-2		Genshaw
7	15-1	7	Genshaw
Black Lake Quarry	300	34	Ferron Point
" " "	25-8	34	Ferron Point
" " "	25-5	34	Ferron Point
Ocqueoc Falls	75	31	Ferron Point
Rockport Quarry	500		Rockport
" "	550		Rockport
Kalkaska County***	14538		Traverse

An additional eight specimens were used, but it is known only that they came from the Afton-Onaway area. The location numbers used in this paper are those established by Kell and Smith (1947).

*Location numbers marked with an asterisk are those established by Verhoeven (1948).

**The hyphenated numbers represent specimens collected by Henry Faul (1942).

***This specimen is from the cuttings of an oil well drilled in Kalkaska County. The number given is the SP number of the well, and is on file with the Michigan Geological Survey.

The collection includes corals from the Rockport Quarry limestone, the Ferron Point Formation, the Lower Genshaw Formation, the Killians member of the Genshaw, the Koehler limestone, and the Gravel Point formation, listed in ascending order. Some 35 different specimens were included in the study. However, certain forms were studied by oriented serial sections, so that the total number of sections examined is approximately one hundred. The 35 specimens are not distributed uniformly through the stratigraphic column, but instead tend to be concentrated in those formations or members which are most fossiliferous, or in which the most diligent search was conducted. Thus, the Gravel Point is a point of concentration because its outcrops were thoroughly searched, and because it is fossiliferous. In contrast, only a few specimens from the Koehler are included because of the lack of fossils in that formation. Some of the Specimens from the Lower Genshaw are so badly crushed as to be almost useless.

TECHNIQUES OF PREPARATION

The most common method of studying corals is by the use of thin sections. However, the writer finds that sections of standard thickness (0.02mm) are not the most useful, because they are too thin to reveal third dimension.

The thin sections used in this study are from 0.06mm to 0.1mm in thickness, depending on the method of preservation. In those specimens preserved in clear calcite, the sections were made thick, so that the maximum possible relief could be obtained. These are the most satisfactory for direct study, but it is difficult to obtain good photographs of them. If the fossil is preserved in clay minerals, or in calcite sufficiently impure as to be opaque, the slides were cut thinner, but only enough to allow the passage of light. The retention of enough thickness to allow three-dimensional interpretation is of first-order importance. This is especially true in those specimens where precise control of orientation is difficult or impossible.

It was not uncommon to have corallums break into fragments when an attempt was made to cut them on a diamond saw. It was found that there are systems of internal fractures, along which the fossil will part at the slightest strain. To avoid this, the specimens were soaked in liquid resin for from one to two hours. Usually the resin permeated the fractures, and the coral, when cool, was firm enough for handling and processing.

Four different orientations of sections were used. The transverse section cuts the axis of the corallite at approximately 90 degrees. It is difficult to obtain a completely accurate transverse section, and so the term is defined as being a section which cuts the corallite axis at an angle between 85 degrees and 90 degrees.

Transverse-oblique sections are defined as being sections which cut the corallite axis at an angle between 70 degrees and 85 degrees.

The longitudinal section is defined as a plane which either contains the axis of the corallite, or is parallel to the axis. When the section contains the corallite axis, one much-to-be-desired result is the display of septa lying in the plane of the section. Ordinarily the septa are sufficiently sinuous so that at least a portion of one septum is brought into the plane of the section, even though other portions of the section may pass between two septa. Most corallites are somewhat sinuous, and so it is virtually impossible to obtain an ideal longitudinal section for distances along the axis of more than a few millimeters. The usual case is to find perhaps a centimeter of longitudinal section with the section becoming more or less oblique on either side as the axis of the corallite bends out of the plane of the section. Almost all longitudinal sections are in planes parallel to the axis, instead of coinciding with the axis. Such sections are valuable, for they are useful in the interpretation of carinae and dissepiments.

The *longitudinal-oblique section* is defined as a plane which intercepts the axis of the corallite at an angle ranging from five degrees to 30 degrees. The sinuosity of the corallites usually results in a short area of longitudinal section, with longitudinal-oblique portions of the same corallite both above and below the longitudinal portion.

Most of the *Hexagonaria* from the Traverse group are forms with a dome-shaped, or hemisheroidal corallum. The diameter of the colonies averages perhaps 20 centimeters. Some are very much larger, as for example the specimen found at the locality called Silva's Folly. The entire corallum is unknown, but it must have been fairly large, for no perceptible radiation of the corallites from a common center was evident, and yet the fragment obtained had a volume of perhaps 3,000 cubic centimeters.

For these dome-shaped corallums, a standard technique was developed. The sample was first cut in half so that the result was two half-hemispheres (See Plate XI). Usually such a cut revealed a series of more-or less longitudinal sections. If the cut was at an angle to the desired orientation, the face of one of the hemispheres was ground until it was a true longitudinal section. This hemisphere was then placed in the diamond saw and a thin slice was cut off, mounted, and labeled as to orientation.

The other half-hemisphere was then ground to obtain a longitudinal-oblique section oriented at a very shallow angle. This was then sawed as before, and the slice mounted.

Because of the growth habits of these forms, it is impossible to get more than a few corallites in transverse section on one slide, because the radiating habit takes the plane of the section ut of the normal very rapidly. However, large sections have distinct advantages, in that they allow both transverse and transverse-oblique sections of the same corallum to be examined at the same time. Therefore, one of the half-hemispheres is then placed in the diamond saw such that the plane of the saw-cut will be a chord of the arc representing the surface of the original corallum. Several thin slices are then removed and mounted as before. Only the central portion of such sections will be transverse; the entire periphery becomes more and more oblique. The remainder of the corallum was usually ground and polished, and given no further processing.

If the entire corallum was not available, the fragment was examined carefully to insure a knowledge of the direction of the coral axes, and a cut was made normal to this direction. If the proper orientation was not achieved at the first attempt, the surface was ground on a lap

until a transverse section was obtained. Following this a cut was made parallel to the ground surface, and the slice removed and mounted. The transverse surface now serves as a guide for the longitudinal sections, because any plane normal to the transverse surface is a longitudinal section. Because the transverse section may not be precisely normal to the corallite axis, it is usually found that the new section will be somewhat oblique. If so, one of the surfaces is ground until a longitudinal section appears, and a slice is taken off parallel to the ground surface. When other orientations were desired, a surface was first ground with the required orientation, and a slice taken off parallel to that surface. Attempts at cutting the desired orientations without first grinding the appropriate surface led only to unoriented fragments.

Peels were found to be almost completely unsatisfactory. (Swann, 1947). Very small structures, such as dissepiments or carinae, were more often than not lost. Very disconcerting was the discovery that peels sometimes added structures which did not exist! In specimens preserved in calcite, it was found that the contact between two adjacent crystals of calcite dissolved more rapidly than the main masses of the crystals. As a result, the finished peel showed a line between two crystals which was identical with the lines formed by dissepiments.

With this discovery, the whole technique was hastily abandoned.

Polished sections are in most cases the most revealing of all methods of study. When specimens preserved in color-microscope, the impression is one of a casting in clear glass. Inclined light enables the student to see deeply into the structure, and thus relationships are revealed which are almost entirely masked in thin sections. It was with the study of polished sections that many of the intricacies of structure were first detected. These discoveries were then used to establish a set of criteria for use with thin sections, and of such nature that the approximate orientation of random sections could be determined. Before these criteria were developed, only those sections for which exact data on orientation was available were useful. But with the orientation criteria, it was possible to expand the base of investigation considerably, for they made it possible to utilize already-existing thin sections for which no data on exact orientation was available.

INTERPRETATIONS OF STRUCTURE

Carinae:-Amond the structures of Hexagonaria used for the identification of species are the carinae. These are very small, linear masses of skeletal tissue which

grow on the septa. (Twenhofel & Shrock, 1935) Carinae are universally present in Hexagonaria. No specimen, upon careful examination, has been found to lack carinae in any part.

In sections cut normal to the slope of the carinae, they are seen to be an isomorphous series. Of the various forms, the rarest is the crenulate carina, which is a sharp-crested fold in the septum. The form is established without appreciable thickening of the septum (See Plate I-a and XI-b).

When a septum makes a low-angle turn, there is not infrequently developed a thickening of the septa, so that the flexure is reinforced by additional skeletal material. This is the elbow type. (See Plates I-a and XI-b)

The modified elbow form is a half-lozenge grown on one side of a septum only, and with the long dimension of the lozenge parallel to the septum. (See Plates I-a and XI-b)

The lozenge carina is a diamond-shaped structure with its long axis parallel to the septum, and with the points projecting on both sides of the septum. (See Plates I-a and XI-b)

Still another form looks like the cross-beam of a telegraph pole, or the yard-arm on a ship's mast. (See Plates I-a and XI-b)

In longitudinal section, the carinae exhibit similiar diversities. The forms range from straight-line linear occurences, through sigmoid, arched, and even bow-shaped. (See Plates I-b and XII) The form which the carinae will display in transverse section cannot be determined from a lognitudinal section. As a corollary, the form displayed in longitudinal section cannot be determined from transverse sections. Any combination of transverse and longitudinal forms is possible.

The angle at which the carinae intercepts the wall of the corallite is called the <u>mural angle</u>, while the angle at which the carinae extended joins the axis of the corallite is called the <u>axial angle</u>. (See Plate I-b) The mural angle varies from 90 degrees to about 20 degrees, and the axial angle varies from 90 degrees to approximately 40 degrees.

Several types of carinae can be found on a single septum. Thus, for example, yard-arms may grade into either elbow types, or offset yard-arms, or both. (See Plate XII-b)

Although carinae seem to be strengthening structures on the septa, they are not restricted to the septa, but in some cases project well beyond the axial termination of the septa. Such occurences are best seen in longitudinal-oblique sections, where the extended carinae appear as dots in a row along a line formed by the extension of one of the septa above or below the occurence. (See Plate XII-b)

In longitudinal sections there are many examples of the implantation of a secondary carina between two previously existing, or primary carinae. (See Plate I-c and XIII-a) The primary carinae reach from the corallite wall to the end of the septa, or in some cases beyond, but the secondary carinae are ordinarily present only in the vicinity of the tabularium, and disappear well before they reach the wall. Counts of primary carinae along a wall will result in a lower count than one taken along the edge of the tabularium, where it will include both primary and secondary carinae. (See Plate I-c)

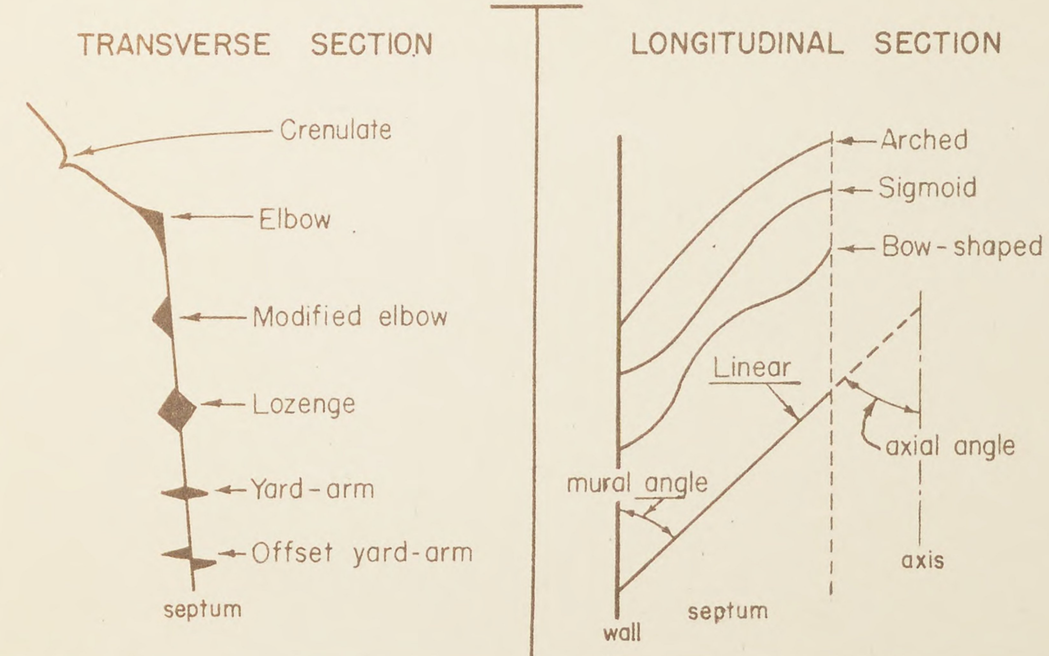
Carinae counts can yield varied results if the orientation of the section is not considered. As an example, (See Plate I-c) a transverse section may result in a low count, because it cuts across the carinae series at an angle. Furthermore, in transverse section it is possible that no carinae will show near the tabularium, because in those highly arched forms in which the axial angle approaches 90 degrees the carinae will be parallel, or nearly so, to the plane of the section. But carinae will show more or less abundantly near the periphery, leading to the erroneous conclusion that carinae exist only near the walls, and that the axial ends of the septa are free of carinae. If the angle at which a transverse-oblique section is cut happens to be the same as the slope of the carinae on one side of the corallite, that side will be without apparent carinae, while the other side of the carinae will be abundantly carinate, because they will have been cut almost normal to their slope. (See Plates I-c and XIII-b) A corallite which presents abundant carinae on one side and none on the other cannot be interpreted on that evidence alone as being non-carinate on one side. (Stumm, 1949)

Carinae which are cut at shallow angles can easily be mistaken for minor dilations of the septa, and omitted from carinae counts for that reason. This is especially true for the elbow, lozenge, or crenulate types, inasmuch as they are short and stout to begin with, and the distortion produced by the angle of interception of the section increases the length, but not the width. (See Plate II-a)

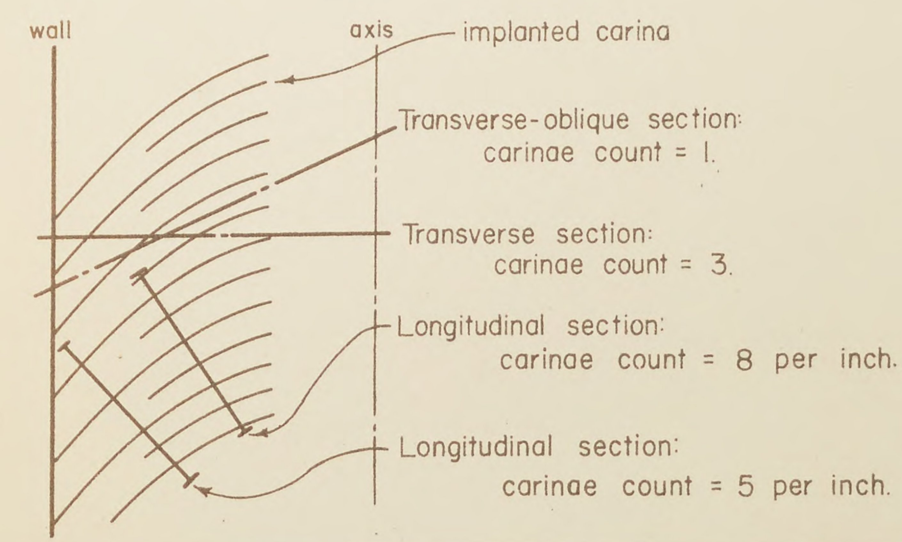
In some places carinae are partially masked by dissepiments, and consequently overlooked in transverse or transverse-oblique sections. There seems to be no inter-relation between carinae and dissepiments. If a section happens to pass through a point where a dissepiment and a carina cross, the appearance will be only that of a slight thickening of the dissepiment where it joins the septum. (See Plates II-a and XIII-c)

TYPES OF CARINAE

TRANSVERSE SECTION / LONGITUDINAL SECTION



IMPLANTATION OF CARINAE and CARINAE COUNTS.
LONGITUDINAL SECTION



Some uniform method of counting carinae would be useful. It is suggested that such counts be made from longitudinal sections only, and only in directions normal to the slope of the carinae. Even this must be used with discretion, for such a count made close to a wall might have a very different result from a similiar count made near the tabularium, because of the implantation of secondary carinae. (See Plate I-c)

If a septum is considered as a plane, and a carina is considered as an intersecting plane, the two structures will be perpendicular to each other. In a longitudinal section, which passes only through the dissepimentarium of a corallite, the carinae will appear to be perpendicular to the septa on those septa which are normal to the plane of the section. However, the carinae on those septa which are at an angle to the plane of the section will no longer appear to be normal to the septa, Reverting to geometry, this effect is the result of passing a plane through two mutually perpendicular planes in such fashion that the third plane is normal to neither of the first two. When this condition is met, the trace of the two mutually perpendicular planes on the third plane will result in the angles of two opposite quadrants being less than 90 degrees, while the other two angles will be greater than

90 degrees. In this case, the third plane is represented by the plane of the longitudinal, or longitudinal-oblique section, and the two mutually perpendicular planes are the carina and a septum. A longitudinal-obluque section illustrates this property to best advantage. In such a section, the tabularium will appear as an elongate oval, with the long axis parallel to the corallite axis. Both immediately above and below this oval, the septa will have been cut so that the plane of the section is normal to the septa, and so the carinae will present their usual appearance. At either side of the oval, between the tabularium and the wall, there will be septa which will have been cut almost co-planar, and so the carinae will appear as sloping lines on the septa. Between these two extremes there will be septa cut at all angles from 90 degrees to zero degrees, and the carinae on these septa will depart more and more from the normal noted at the 90 degree point, and will approach the attitude seen in a section co-planar with a septum, which is reached at the zero degree position. (See Plate XIV-a)

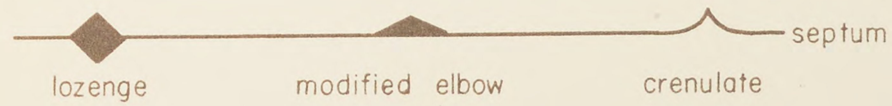
Walls:-In most Hexagonaria the walls are composed of three layers of material; a thin, central, opaque lamination, and a much thicker layer of translucent material on either side of the opaque central layer (See Plate III-a). The entire wall may vary in thickness from

PLATE II

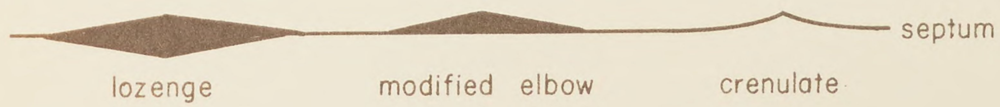
CARINAE
MODIFICATIONS DUE TO ORIENTATION

(a)

Appearance of various forms in a section cut normal to their slope.

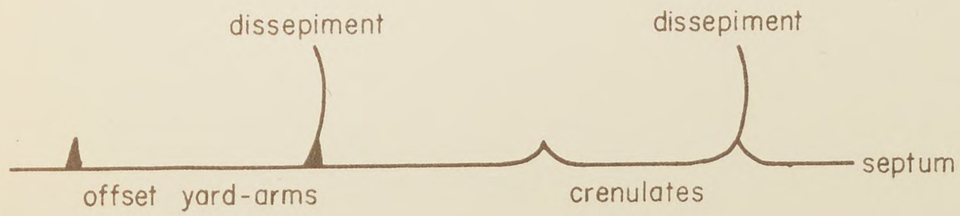


Appearance of the same carinae in a section cut at a shallow angle to their slope.



CARINAE MASKED BY DISSEPIMENTS

(b)



as little as 0.2mm to as much as 1.0mm

Walls range from straight or curved to strongly serrate, or zig-zag. In many instances this variation seems to be a function of the manner in which the septa join the walls. If the septa of two adjacent corallites meet the wall base-to-base, the wall will be straight or curved, but rarely if ever serrate. However, if the septa are offset along the wall, the walls tend to be serrate. (See Plates III-b and XIV-b)

The gross appearance of serration is present in some cases where close examination reveals the wall, as represented by its opaque central lamina, to be straight or somewhat sinuous. This pseudo-serration is caused by the deposition of translucent skeletal material about the base of each septum. In this case, if the septa meet the wall in offset fashion, the gross appearance is that of a strongly serrate wall. (See Plates III-c and XIV-b)

Septa:-Some specimens show a dark central layer in the base of the septa. (See Plate XIV-b) Such an occurance is by no means universal. Many specimens are utterly lacking any internal septal structures, and even in those cases where the central lamina is present, it may not be found throughout the corallite. Many variations occur, from well-defined lines to shadowy areas in the base to uniform, translucent, featureless structures.

The septa range from straight to crenulate, with all intervening degrees of sinuosity. This is true whether they are examined in transverse or longitudinal section.

Septal dilation:-Corals have an annual cycle of growth, such that it produces an effect much like tree rings. (Faul, 1942) Every structure in the coral skeleton is thickened in cyclic fashion, but the walls and septa are affected to a much greater degree than the more delicate structures such as dissepiments and tabulae. (See Plate XIV-c) The thickened portion of the septum is not a geometrically perfect figure, but rather is controlled and modified by local deviations. As the animal grows upward during the period when the skeleton is being thickened, the dilated portion conforms to the profile of the calyx. Thus, the wall side of the thickened septa will be higher than the axial ends, for the axial ends were depressed into the calicular pit. (See Plates IV and XIV-c) Such growth rings have important effects on the appearance of transverse sections.

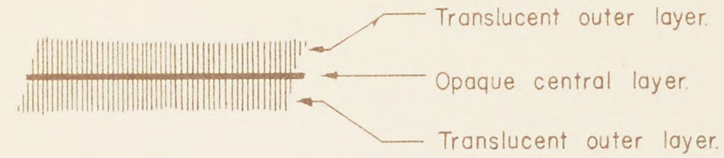
Should a transverse section be cut such that it just nips the peripheral portion of the thickened area, that septum will show mural dilation. (see Plate IV) If however, the section cuts the thickened portion through the middle, the entire septum will be dilated, but if the section cuts through the axial portion of the thickening, the septum will be axially dilated.

Because these growth rings are cyclic, it is quite possible to obtain a transverse-obluque section which cuts the thickened part on one side of the corallite, and pssses neatly between two growth rings on the other side of the corallite. Result: septal dilation on one side of the corallite, and none on the other. (See Plate IV) Further, because the growths are not entirely regular, it is common to find all combinations of these conditions in a single corallite. Transverse serial sections cut only a few millimeters apart demonstrate that the nature of septal dilation may change within a very small vertical, as well as horizontal distance.

Size and numbers of septa:-Because of the known relationship between size of animal and structural organization, a comparison was made between the cross-sectional area of corallites and the numbers of septa which each contained. The areas were obtained by the use of the nomogram on Plate VIII of this paper, and the septa were carefully counted and tabulated. Care was taken so that only mature corallites were used, and only transverse sections were used so that the true cross-sectional area would not be greatly distorted. The result is in cluded in Plate V and VI).

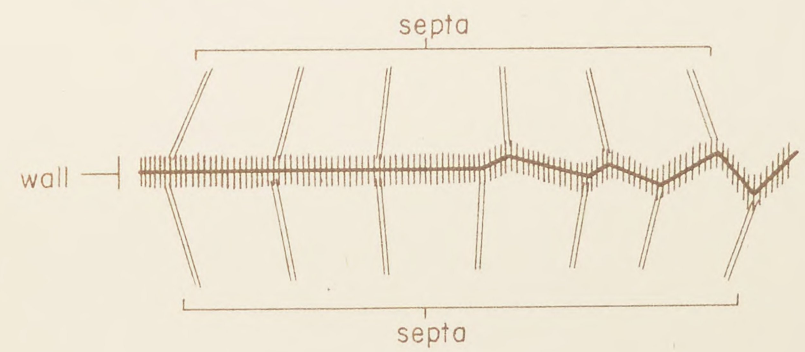
It would seem that there is a distinct correlation between cross-sectional area and the number of septa.

(a) SECTION OF WALL BETWEEN TWO CORALLITES



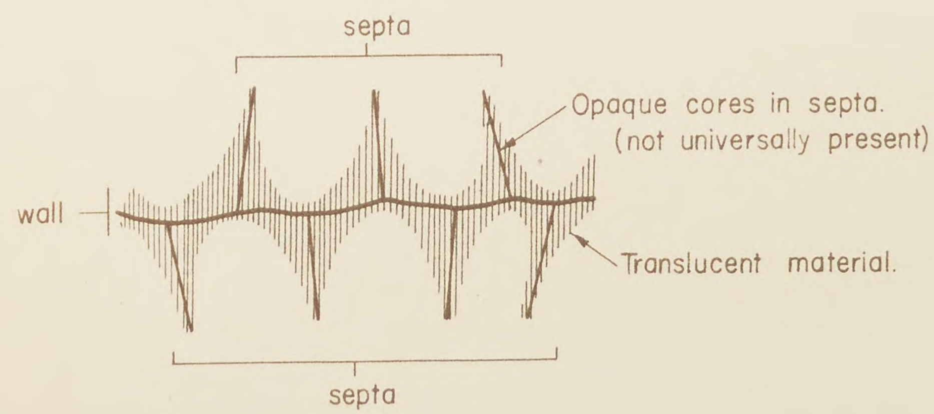
Magnification x 30

(b) RELATION OF SEPTA TO WALL SERRATION



Magnification x15

(c) PSEUDO-SERRATE WALL

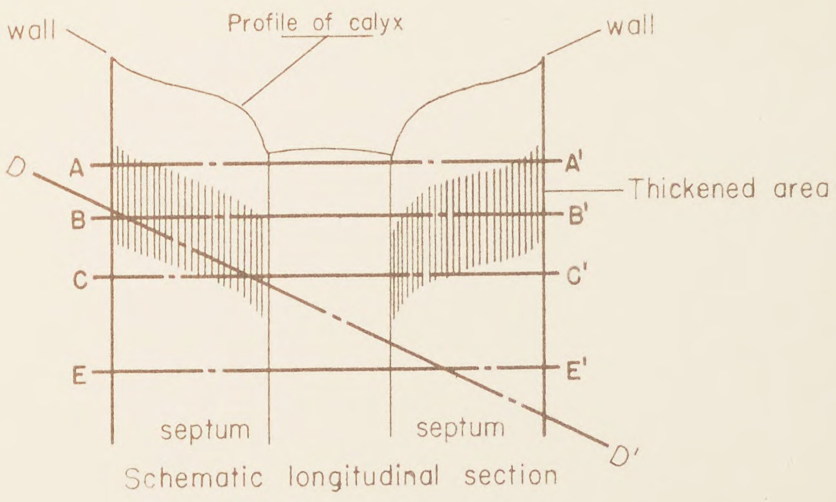


Magnification x 20

This receives further confirmation from a specimen collected in Afton Quarry. (See Plate XV-a) In this coral, a large corallite was forced to reduce its size. Accordingly, a new wall was formed which is completely separated from any other structure except two of the original septa. In the abandoned portion the skeleton contains 17 septa, while in the newly-formed section of wall there are ten septa. The odd number of septa is accounted for by an intricate arrangement of anastamozed septa at one end of the new wall. Reduction in area equals reduction in the number of septa.

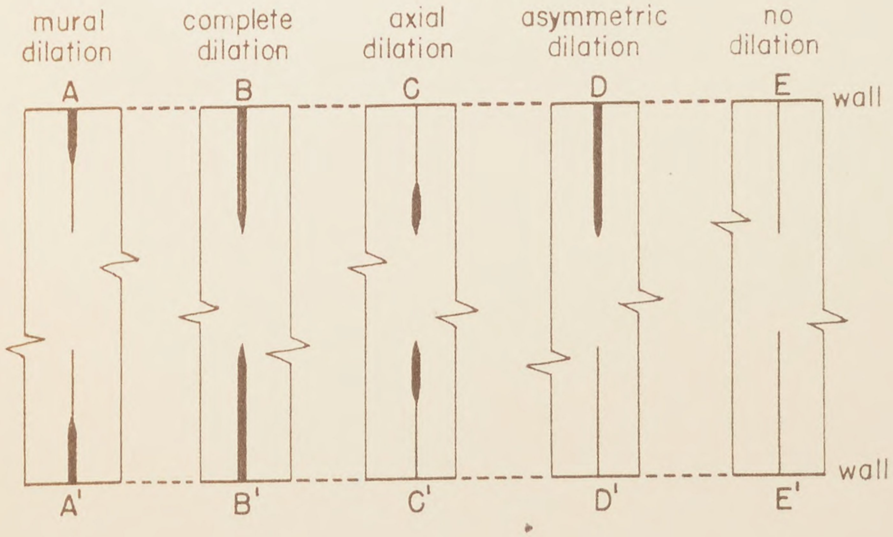
As a corollary, it seems likely that a corallite must add additional septa as it grows larger. The process by which this is accomplished is uncertain. However, there is a suggestion in a specimen from the Gravel Point. In this coral, the dissepiments between two widely-spaced septa have developed a compound structure which in turn is developing a straight central portion mid-way between the two original septa. This implanted structure might well be the inception of a new septum, which will eventually extend itself to both the wall and the tabularium. No exception to the rule of even numbers of septa has been found, and so it appears probable that two new septa must be developed simulatneously, or nearly so. No trace of the hypothetical second septum has been noted in the specimen described.

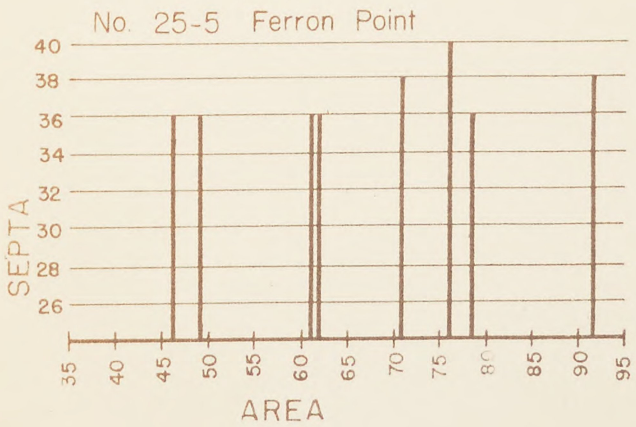
"GROWTH RINGS" and SEPTAL DILATION

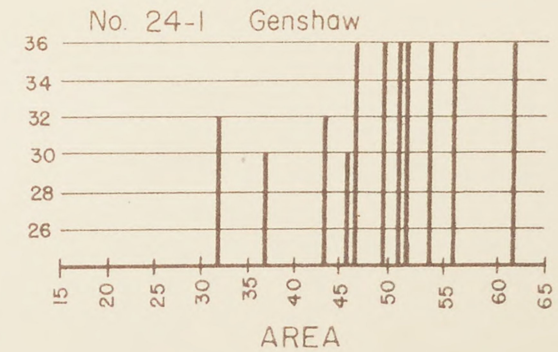


AA', BB', CC', DD', EE' = Traces of variously placed and oriented transverse sections.

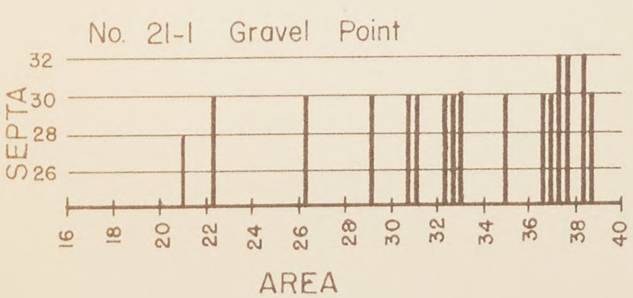
DIAGRAMMATIC APPEARANCE OF SEPTA IN TRANSVERSE SECTION

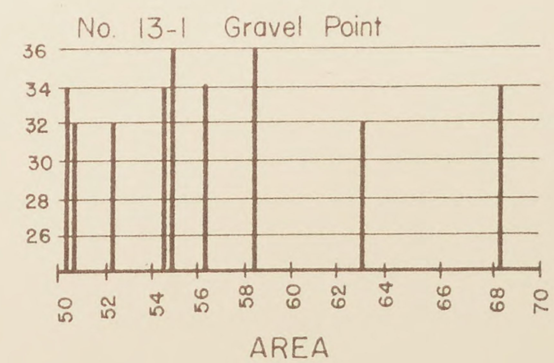


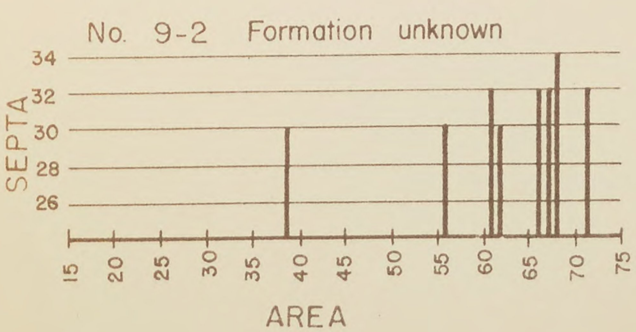


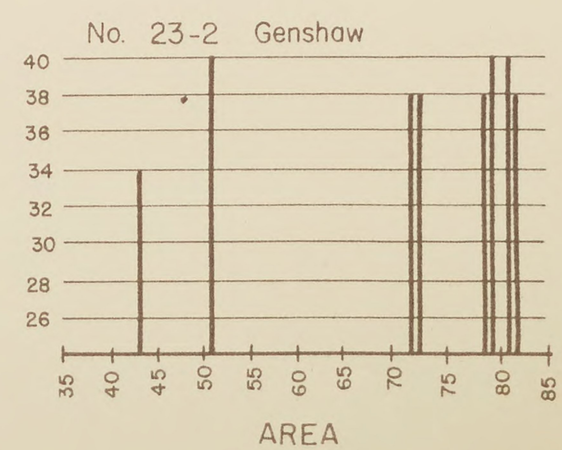


AREA = Cross-sectional area of corallites in square millimeters.









Dissepiments:-Dissepiments appear in transverse sections as very fine, curved traces joining adjacent septa. They are usually a simple curved line, but this pattern may be elaborated to include compound dissepiments in which a second structure joins the first. (See Plates V-a and XV-c) In longitudinal sections, the dissepiments are seen to bound small, globose dissepimental chambers. If the dissepiments are simple, the chamber will be bounded on two sides by adjacent septa, and on the other sides by dissepiments. If the dissepiments are compound, then the chamber is bound on only one side by a septum, and all other sides are bound by dissepiments. These chambers may be either horizontal or inclined, depending on the attitude of the longest diameter as seen in longitudinal section. (See Plate V-b) Some patterns are sufficiently regular in longitudinal section to warrant the description "scale-like". (See Plate XVI-a) Others are extremely diverse. Some corallites present patterns in which the chambers will be horizontal in one portion of the corallite, and incline in another. (See Plate XVI-a)

Size of dissepimental chambers is defined as being the length of the longest diameter, regardless of the orientation of the chamber. Size is variable within wide limits within the same corallite. One specimen includes chambers which range in size from 0.2mm to 1.0mm (See Plate XVI-b).

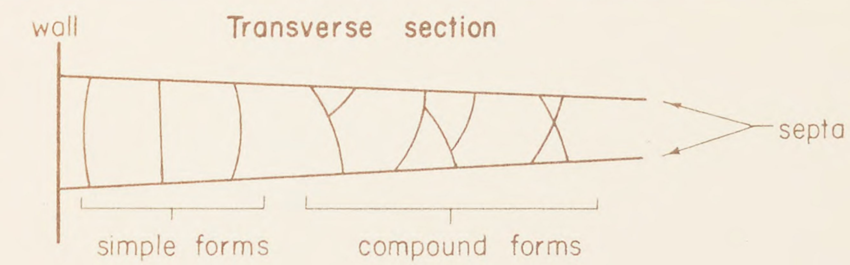
If the chambers in a coral are horizontal and regularly disposed, then a transverse section will show the dissepiments as generally regular spaced, but with the arch alternately pointing axially and peripherally. However, if the specimen is transverse-oblique, the same dissepiments will tend to display a consistent peripherally-pointed arch on one side of the corallite, and an axially-pointed arch on the other side. (see Plate VII-c) Because such regularity as is displayed in the diagram is rarely found in nature, it follwos that the two instances cited are the limiting cases, and only generalizations or approximations of them should be sought. Irregularities in structure, such as variation in size or attitude can develop many and varied patterns.

Some septa which project into the tabularium appear to be connected by dissepiments right up to the distal end. (See Plate XV-b) Examination in longitudinal section discloses that these traces are in reality tabellae, but tabellae which are nothing more than dissepiments which terminate on a tabula rather than on another dissepiment. Tabellae are probably only variations of the dissepiments.

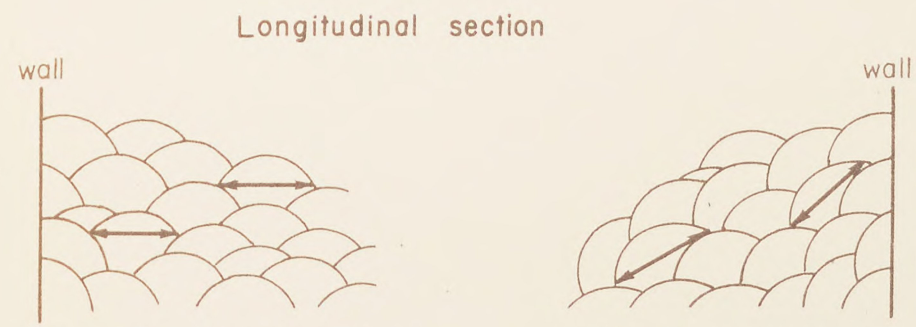
The apparent concentration of dissepiments around the tabularium of some forms is an effect produced by the approach of the septa to a common center. (See Plate VIII)

DISSEPIMENTS

(a)



(b)

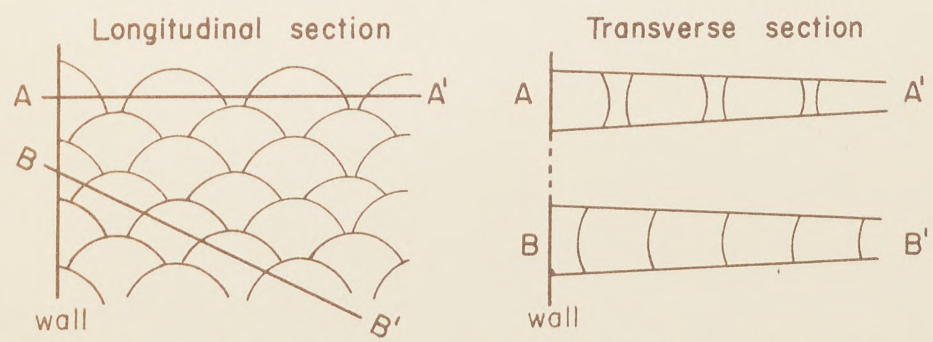


Horizontal dissepimental chambers.

Inclined dissepimental chambers.

Arrows indicate greatest diameter of chambers. This is the dimension used in measurement.

(c)



Function of orientation as a control of direction of curvature.

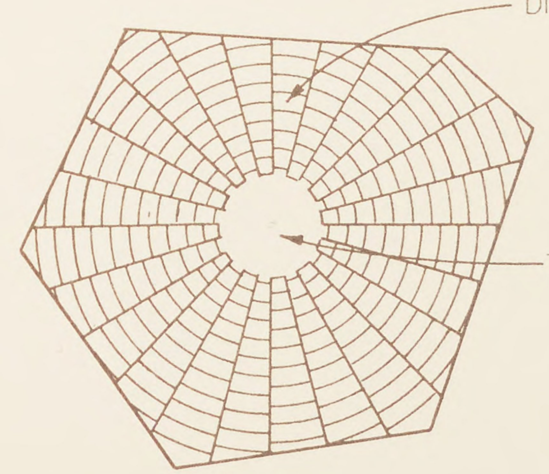
Careful measurements should be taken in the longitudinal section to determine whether there is actually a grouping of dissepiments around the tabularium. Such a grouping may be produced in transverse section without decreasing the size of the dissepimental chambers. If the chambers in that portion of the dissepimentarium close to the wall are horizontal, but those in the portion near the tabularium are inclined, there will be a real concentration of dissepiments about the tabularium. (See Plate XVI-a) Sanford (1939) defines dissepimentarium as a peripheral zone of dissepiments. Of course, the same effect can be produced by a reduction in the size of the chambers.

The presence of compound dissepiments in a transverse section is not proof positive that compound dissepimental structures are actually present. Compound dissepiments can be duplicated from simple ones in transverse-oblique sections. If the plane of the section intercepts the line along which two simple dissepiments join, the resulting trace will be Y-shaped. (See Plate IX-a)

In some instances, the dissepiments are increasingly complex near the wall. This is particularly true if the adjacent septa are spread widely apart so that the dissepimental tissue must fill a comparatively large volume of space. These structures become so complex that the distinction between dissepiments and cystosepiments is largely lost. Such occurences imply that the two types of structure

PSEUDO-CONCENTRATION OF DISSEPIMENTS

(a)



All dissepiments are 0.1 inches apart. Note the apparent concentration about the tabularium.

are produced by the same mechanism in the coral animal. Because of this relationship tabellae, dissepiments, and cystosepiments should probably be thought of as being members of an isomorphous series.

If the dissepiments are steeply arched, a transverse section will usually show the traces as a broad, indistinct line. (See Plate IX-b) Such broad, but correspondingly faint areas are frequently overlooked when dissepiment counts are made. The lack of dissepiments in transverse section is not in itself proof that the fossil is free of these structures. A transverse-oblique section will ordinarily reveal abundant dissepiments, even when they are not evident in transverse section. Measurements of dissepiments should always be made from longitudinal sections.

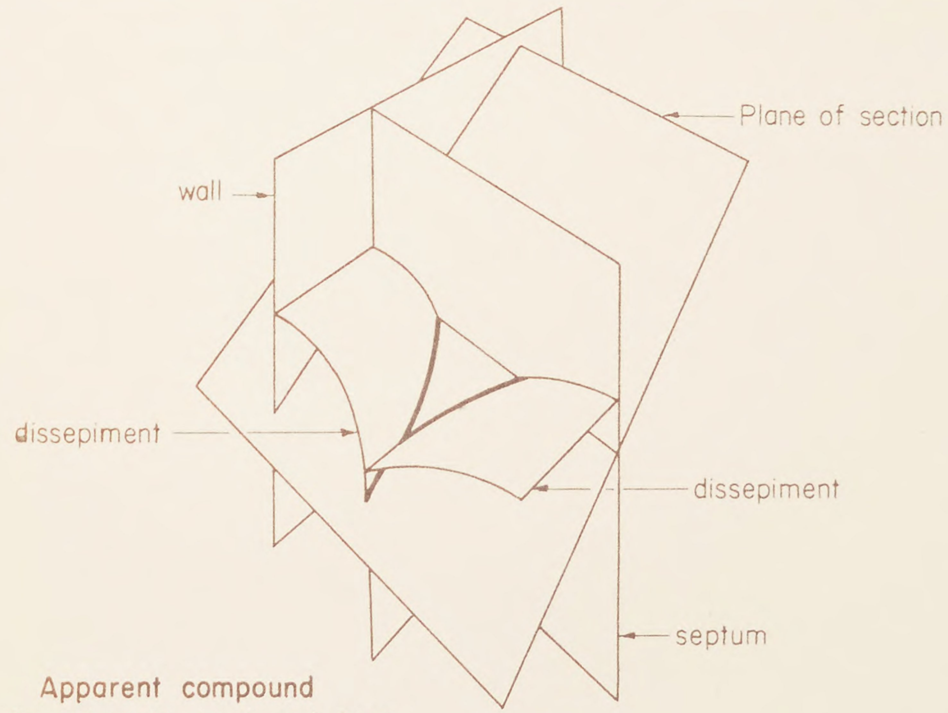
<u>Orientation Criteria</u>:-From the preceding discussion, it is possible to develop criteria for the determination of the approximate orientation of random sections. It has already been demonstrated that this is of primary importance because of the danger of making false determinations on the basis of a series of misinterpreted structures.

In transverse section:

1)-Carinae may be absent or few near the tabularium, but relatively clear and numerous near the wall. They will be uniformly present, although superficially perhaps absent, around the entire corallite.

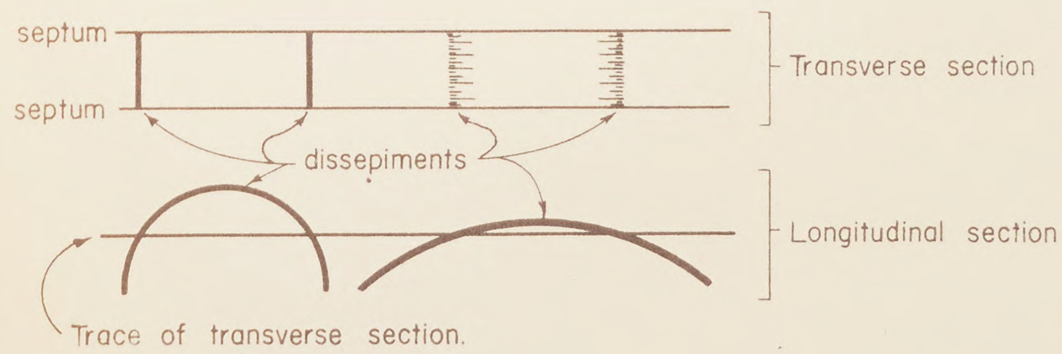
DISSEPIMENTS

(a)



Apparent compound dissepiments produced from simple dissepiments by an oblique orientation of the section.

(b) Orientation as a factor in the apparent thickness of dissepiments.



2)-Dissepiments will generally be simple types. If compound forms occur, they will be distributed more or less at random over the entire corallite, and will not be concentrated in two opposite quadrants. (See plate XVII)

3)-If there is a grouping of dissepiments, the grouping will be consistent around the entire corallite.

4)-If septal dilation is present, it will usually be uniform around the entire corallite. Unfortunately, irregularities in the structure of the animal may partially invalidate this criterion.

5)-There will be approximately the same number of dissepiments per unit of dissepimentarium on all sides of the corallite.

In transverse-oblique section:

1)-Carinae will be abundant on one side of the corallite, but few or absent on the other side; or, if the carinae are short and stout on one side and thin and tall on the other, the section will be only slightly oblique.

2)-Dissepiments will tend to show concentrations of compound types in two opposite quadrants.

3)-The number of dissepiments per unit of dissepimentarium may be slightly different on opposite sides of the tabularium. This criterion is valid in only the limited number of cases where dissepimental chambers are either consistently inclined, or consistently horizontal.

4)-If the dissepimental chambers are inclined near the tabularium and horizontal near the wall, a transverse-oblique section tends to eliminate the grouping of dissepiments in one quadrant.

5)-In extreme cases, the tabularium will be slightly oval.

In longitudinal-oblique section:

1)-The tabularium will be an elongate oval, with its long axis parallel to the walls.

2)-The carinae will be at right angles to the septa both above and below the two apices of the oval tabularium, but will depart from the normal more and more as the short axis of the tabularium is approached.

3)-Carinae will be relatively abundant on the septa beyond one apex of the tabularium oval, but relatively rare beyond the other apex.

AREA NOMOGRAM

Paleontologists have been accustomed to measure the size of Hexagonaria by means of a relation called average diameter. The quantity is defined as the arithmetic mean of the longest and shortest dimension, taken roughly at right angles to each other. (Faul, 1942)

Biologists have long known that the morphology of animals is at least in part a function of the mass of the animal, because it is the mass which controls such things as the strength of the structural members. The mass of animals is directly proportional to the volume, and so it follows that any attempted correlation between morphological characteristics and size must be made on the basis of volumetric considerations. Fortunately, the colonial coral is essentially a tubular animal, and for this reason the volume of the animal is directly proportional to the cross-sectional area.

The average diameter is not proportional to the cross-sectional area of Hexagonaria. If a square two inches on a side is measured, using average diameter, the resultant average is two inches. If a rectangle four inches long and one inch wide is measured in the same way, the resulting average diameter is two and one-half inches. And yet the areas of both figures are the same! Further, if our rectangles were the tops of solid blocks four inches high, the volume would in each case remain the same. Average diameter is not proportional to volume.

These considerations make it obvious that average diameter is not a valid measurement of size. A direct measurement of cross-sectional area would be ideal, because the volume of a coral is directly proportional to its cross-section. However, measuring areas directly with a planimeter is exceedingly laborious, and so an easier method was sought. A nomogram (Plate X) was developed which yields rather close approximations to the true values. It involves measuring two dimensions at right angles to each other, and such that the lines bisect each other. The greatest length is chosen for one, and the other is allowed to fall where it may. The method is based on the observation that most Hexagonaria are irregular hexagons. It is obvious that the results achieved by the nomogram are only approximations, but it is believed that they are sufficiently accurate to warrant future usage.

CONCLUSIONS

Amond the specific criteria used to identify Hexagonaria are the following: the character of the wall, whether straight or serrate; the shape, number, and mode of occurence of dissepiments; the average diameter of the corallites; the number and nature of the carinae; and the number and nature of the septa.

The interpretation of these structures with respect to solid geometry has been somewhat neglected. Geometric considerations indicate that the shape of the carinae, as

PLATE X

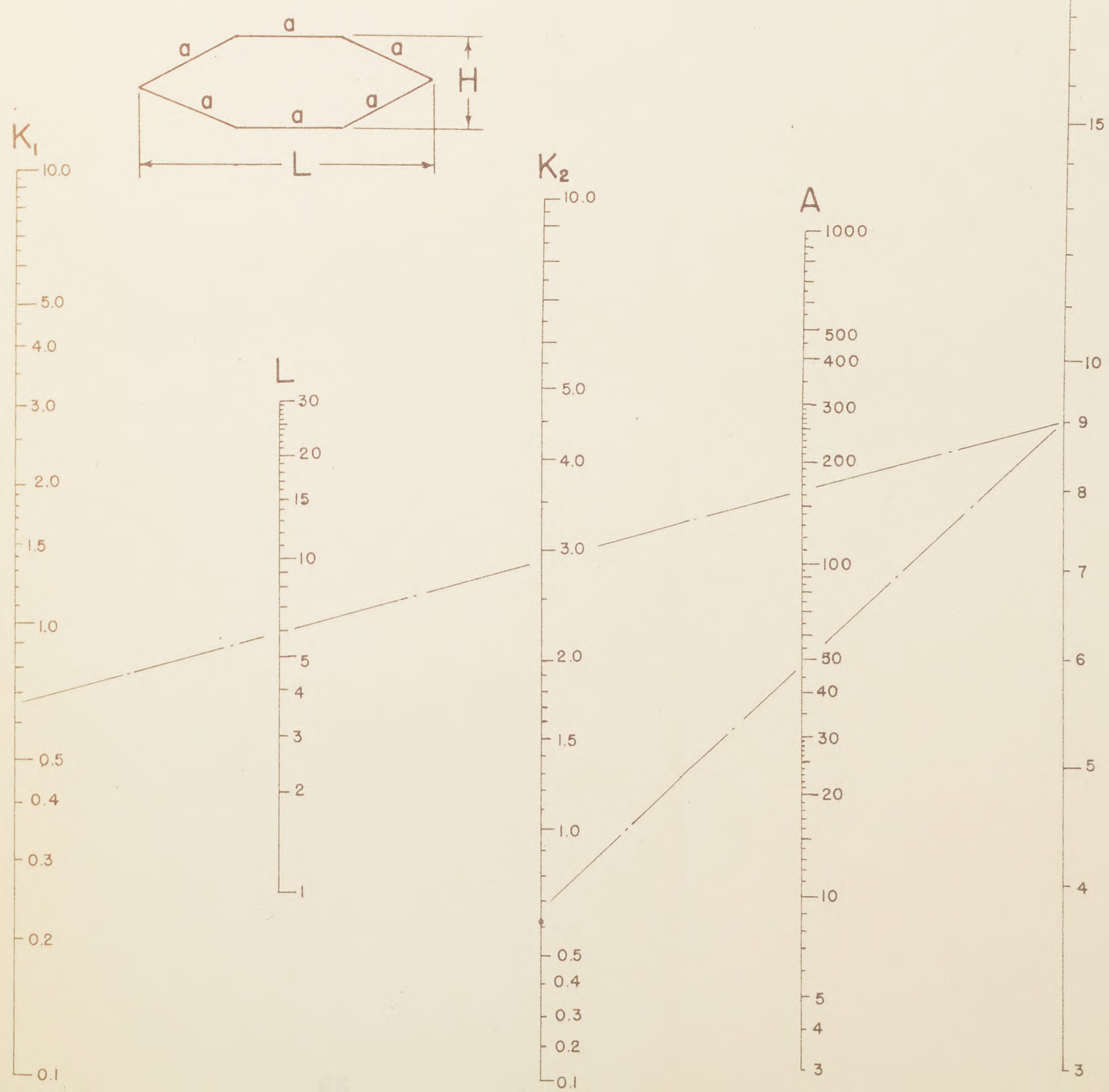
Nomogram for the area A of a semi-regular hexagon in square units, in terms of "Height" H and "Length" L.

Method of use:

1)- First index line from H to L determines K_1

2)- Find $K_2 = K_1$

3)- Second index line from K_2 to H determines area A



well as their numbers, are considerably modified by the orientation of the plane of the section being studied.

The same is true of dissepiments, for their direction of curvature, their number and spacing may be altered by a comparatively slight change in the orientation of the study section.

In many cases the dilation of septa appears to have little value, because the dilation is controlled by the orientation of the section with respect to growth lines, and perhaps any other structural modification which results in a thickening of the skeletal structures. Certainly septal dilation as a specific criterion should be used with caution.

It appears that the average number of septa has little value in specific determination, because of the correlation between the size of the corallites and the numbers of septa. It is easily possible, for example, that an entire colony might be stunted by turbid water, and thus display a consistently lower number of septa per corallite than a more advantageously located colony a short distance away.

The nature of the wall is of doubtful value because of the control exercised by the septa, and also because of the development of pseudo-serrate walls, which serves to mask the true nature of the structure.

Most identifications of *Hexagonaria* have been based upon the examination of sections the orientation of which have been assumed to be identical, i. e., perpendicular to the axis or parallel to the axis. This laboratory study applying defined orientations of sections suggests that a re-examination of established species would be desirable.

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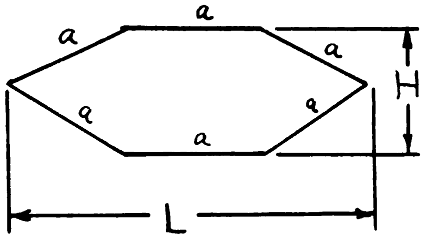
APPENDIX

Derivation of Area Nomogram:



Let L equal length of a semi-regular hexagon, and let H equal the height of such a hexagon, and let a equal the lengths of the sides.

Then $L = a + \sqrt{4a^2 + H^2}$.

Solving for $a = \frac{1}{3}\left(\sqrt{4L^2 + 3H^2} - L\right)$,

then $\frac{H}{2}(a + L) = A = \frac{H}{6}\left(2L + \sqrt{4L^2 + 3H^2}\right)$.

Setting $L = KH$, then $A = \frac{H^2}{6}\left(2K + \sqrt{4K^2 + 3}\right)$

Writing both in logarithmic forms, and then in determinate forms, which suggests an alignment chart:

$$\begin{vmatrix} 0 & \log K & 1 \\ 1 & \frac{1}{2}\log L & 1 \\ 2 & \log H & 1 \end{vmatrix} = 0, \qquad \begin{vmatrix} 2 & \log H & 1 \\ 3 & \frac{1}{4}\log 6A & 1 \\ 4 & \frac{1}{2}\log\left(2K + \sqrt{4K^2 + 3}\right) & 1 \end{vmatrix} = 0$$

Let H vary from 1 to 10, and L from 1 to 100, then

$x_1 = 0$, $y_1 = \log K$; K:(-1, 100); y :(-1, 2).
$x_2 = 1$, $y_2 = \frac{1}{2}\log L$; L:(1, 100); y :(0, 1).
$x_3 = 2$, $y_3 = \log H$; H:(1, 10); y: (0, 1).
$x_4 = 3$, $y_4 = \frac{1}{4}\log 6A$; A:(.32, 666); y :(.07, 1.15)
$x_5 = 4$, $y_5 = \frac{1}{2}\log\left(2K + \sqrt{4K^2 + 3}\right)$; K:(.1, 100); y :(.14, 1.3).

But this shape is inconvenient, and a chart with better proportions results from the following modifications:

$$\begin{vmatrix} 0 & 3\log K \;\; 3 & 1 \\ 1.75 & \frac{9}{4}\log L \;\; \frac{9}{4} & 1 \\ 7 & 9\log H & 1 \end{vmatrix} = 0, \qquad \begin{vmatrix} 7 & 9\log H & 1 \\ 5.25 & \frac{9}{4}\log 6A - .65 & 1 \\ 3.5 & \frac{9}{4}\log\left(2K + \sqrt{4K^2 + 3}\right) - 1.3 & 1 \end{vmatrix} = 0$$

The new scales are:

$x_1 = 0$, $y_1 = 3\log K + 3$; K:(.1, 100); y :(0, 9).
$x_2 = 1.75$, $y_2 = \frac{9}{4}\log L + \frac{9}{4}$; L:(.1, 1000); y :(0, 9).

$x_3 = 7$, $y_3 = 9\log H$; H:(1, 10); y :(0, 9).
$x_4 = 5.25$, $y_4 = \frac{9}{4}\log 6A - .65$; A:(.32, 667); y :(0, 9.71).

$x_5 = 3.5$, $y_5 = \frac{9}{4}\log(2K + \sqrt{4K^2 + 3}) - 1.3$; K:(1, 100); y :(0, 10.42).

Hence the chart will occupy a space 7 inches wide and 1o.5 inches tall. With the range of the scales suitably modified, the resultant chart will be found on page 39 of this paper.

PLATE XI

ORIENTATION OF SECTIONS (a)

The white planes in the figure indicate the planes of diamond-saw cuts used to obtain oriented and serial sections.

TYPES OF CARINAE (b)

Yard-arms

Lozenges

Elbows

Crenulate

PLATE XII

TYPES OF CARINAE (a)

Sigmoid

No. 550

Arched

No. 15

Bow-shaped

No. 200

EXTENDED CARINAE (b)

Note trace of carinae extending beyond the axial terminus of the septa.

No. 550

PLATE XIII

IMPLANTED CARINAE (a)

No. 300

No. 14638

CARINAE IN TRANSVERSE-OBLIQUE SECTION (b)

No. 14638

MASKED CARINAE (c)

No. 450

PLATE XIV

CARINAE IN LONGITUDINAL-OBLIQUE SECTION (a)

No. 200

No. 550

No. 550

WALLS (b)

Only a very faint trace of the laminated wall structure is present in the photograph.

No. 35

GROWTH RINGS (c)

No. 7-6 (After Faul, 1942

PLATE XV

AREA-SEPTA CORRELATION (a)

No. 100

DISSEPIMENTS AND TABELIAE (b)

No. 7-6

COMPOUND AND SIMPLE DISSEPIMENTS (c)

compound— —simple

No. 35

PLATE XVI

DISSEPIMENTAL CHAMBERS (a)

No 450

Chambers peripherally horizontal, axially inclined. Pattern regular, or scale-like.

SIZE RANGE OF DISSEPIMENTAL CHAMBERS (b)

No. 100 No. 15

Note that the size range of the dissepimental chambers is very great in these specimens.

PLATE XVII

DISSEPIMENTS IN TRANSVERSE-OBLIQUE SECTION

simple dissepiments
in these quadrants

compound dissepiments
in these quadrants

No. 450

Note the tendency of the compound dissepiments to concentrate in two opposite quadrants. This is a criterion to establishing the section as transverse-oblique.

PLATE XVIII

SERIAL SECTIONS

Specimen No. 450

ROOM USE ONLY