

GROWTH CYCLES AND PALEOECOLOGY

OF

DEVONIAN RUGOSA

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ABSTRACT

Solitary rugose corals of the Middle Devonian Hungry Hollow Formation exhibit annual, synodic month and diurnal periodicities of their epithelial growth lines. Annual cyclicity is poorly developed due to the slight seasonal variation of the 33°S paleolatitude. Thirteen monthly bands each with a mean of 30.38 diurnal lines comprise a Middle Devonian year of approximately 395 days. Corallite measurements yielded a monthly vertical growth rate of .377 cm. A major correlative reduction in monthly growth is apparent at approximately seven monthly bands from the apex. Environmental deterioration probably accounts for this reduction and the randomly occurring disturbance lines visible on the epithecae. Random periods of rejuvenescence in which the corallite diameter is reduced may be linked to abnormal environmental conditions. Bryozoan larvae actively settled on corallite areas which provided shelter from abrasion, water currents and light. The growth of the corallites is anisometric and exhibits no apparent relationship between monthly growth rate and diameter increase.

The frequent occurrences of geniculate corallites in the sample are indicative of occasionally turbulent water conditions that toppled the immature corallites.

Storms probably created turbulence that toppled much of the coral population with heights of 2.0-4.0 cm and resulted in subsequent geniculation. An exceptionally violent storm probably destroyed the shallow epicontinental sea habitat of the rugosa by intense wave action. The skeletal debris was transported inland and deposited unconformably on the lime mud of the carbonate platform. When conditions normalized, lime mud was deposited onto the fossiliferous shale unit.

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List of Symbols

CORR. COEF. = Correlation Coefficient

G = Genticulation

N = Number of Sample Population Elements

R = Rejuvenescence

S_x = Sample Standard Deviation

\bar{X} = Sample Population Mean

Chapter 1 - Introduction

1.1 Statement of Problem

The highly fossiliferous coral zone of the Hungry Hollow Formation near Arkona, Ontario provides an ideal sampling location for rugose corals serving an investigation of growth lines. Such an investigation was performed to define general growth rhythms and characteristics of the rugose coral population represented in the Hungry Hollow Formation. The growth lines were also used in conjunction with other characteristics of the corals and the formation in an attempt to define the ecological and sedimentological conditions of the Hungry Hollow Formation.

I carried out the field work during the summer of 1983. The purpose was to ascertain the sedimentological history of the formation and to collect specimens of solitary rugose corals for laboratory examination. These specimens were concentrated in the shale beds of the formation. Figures 1-3 show the study area and sample locations. The outcrop is also shown in plates 1-4. Other features of the formation regarding lateral extent, thickness, lithological and fossil content were also noted. A measured stratigraphic section of the outcrop in Hungry Hollow is shown in figure 3. The specimens were cleaned and

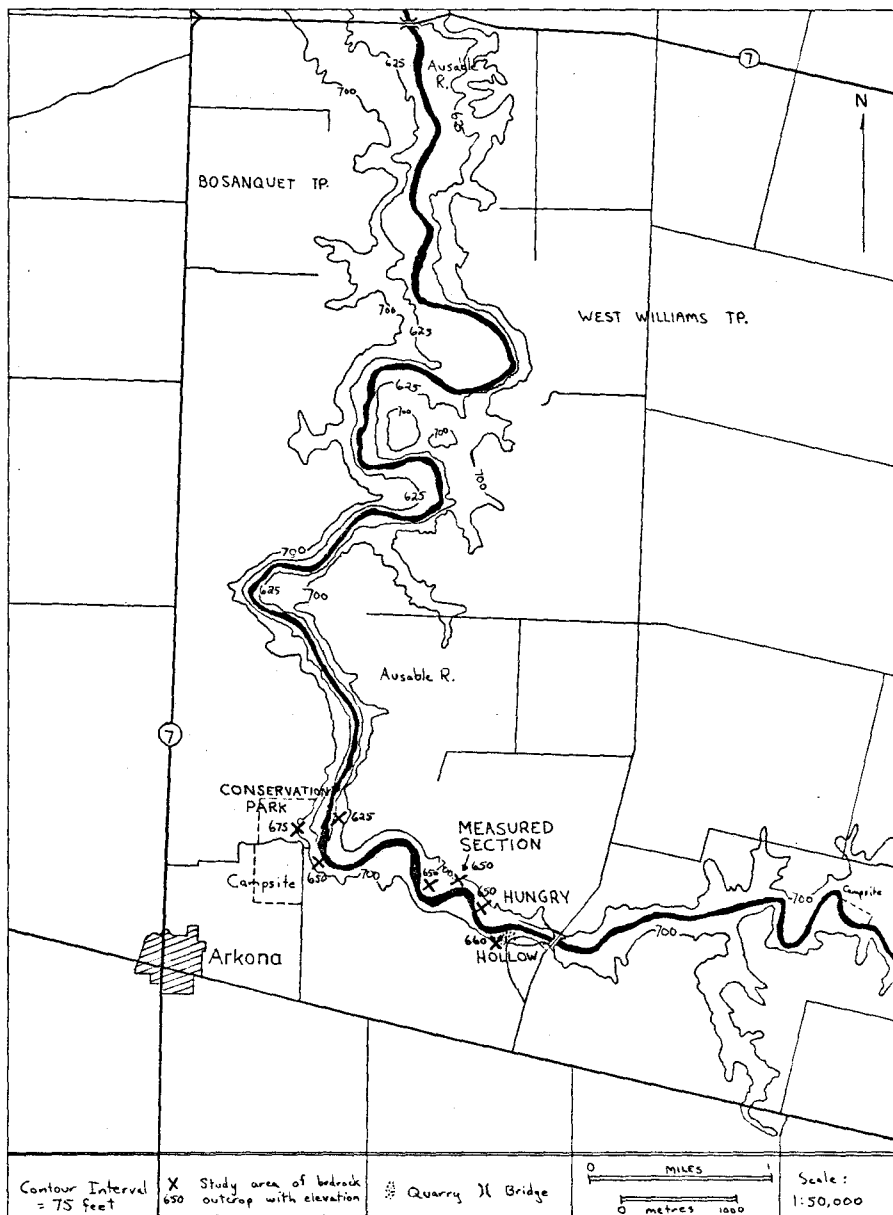


Fig.2 STUDY LOCATIONS MAP

numbered according to their sample location.

1.2 Physiography and Geology of the Study Area

The study area was the Ausable River watershed in Lambton County near Arkona, Ontario (figs 1,2). The area is a gently rolling till plain known as the Wyoming till moraine. The Ausable River has cut a steeply sided valley through the glacial till to depths of 25 m and exposed the fossiliferous limestone and shale of the Widder, Hungry Hollow and Arkona Formations of the Middle Devonian (Gevetian) Hamilton Group (fig. 3). Of these, the Hungry Hollow Formation is most highly fossiliferous, both in abundance and diversity of invertebrates.

The Hamilton Group according to Hewitt (1972):

<u>Group</u>	<u>Formation</u>	<u>Thickness</u>	<u>Lithology</u>
Hamilton c. 117m	Ipperwash	28.7 m	grey limestone
	Widder	13.7 m	grey shale and limestone
	Hungry Hollow	2.0 m	grey limestone and shale
	Arkona	36.6 m	grey shale
	Rockport Quarry	3.0 m	grey argillaceous limestone
	Bell	18.3 m	grey shale
	Marcellus	15.0 m	black shale

The Marcellus Formation lies unconformably on the underlying Seneca Limestone of the Onandaga Formation. Uplift and subsequent erosion of the Marcellus Formation created an erosional unconformity upon which the Rockport Quarry Formation was deposited. Thickness of the Hamilton Group is 90 m near southern Lake Huron where it borders on the Michigan Basin and decreases in thickness to the east.

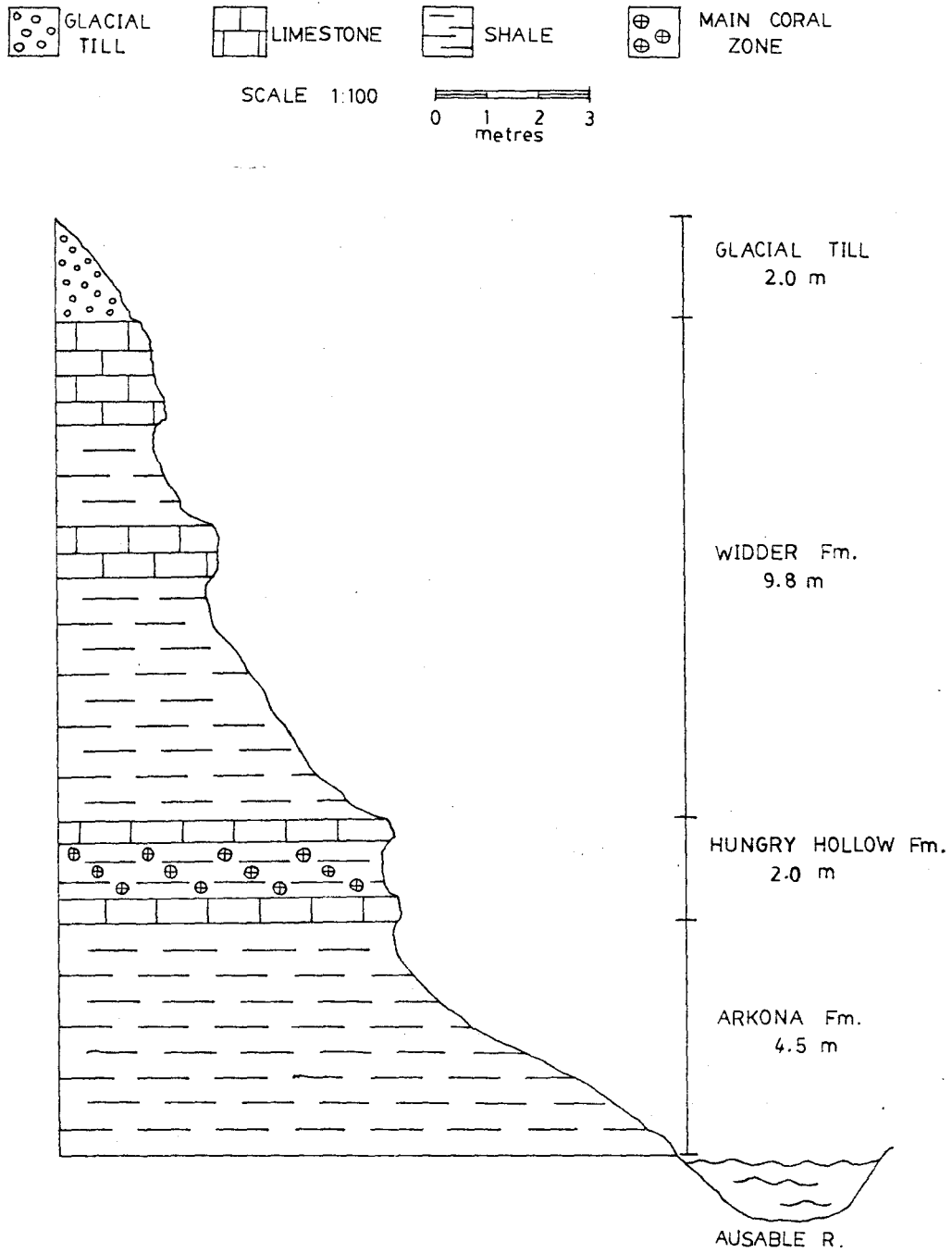


FIG3 STRATIGRAPHIC SECTION, HUNGRY HOLLOW

Plate 1: Outcrop along the North bank of the Ausable River showing the Widder (W), Hungry Hollow (HH) and Arkona Shale (AS) Formations.

Plate 2: The shale unit (coral zone) and limestone units of the Hungry Hollow Formation (HH). Note the sharp contacts between units.



Plate 3: The Hungry Hollow Formation. Some iron-oxide staining is visible.

Plate 4: The Hungry Hollow Formation shale beds along with the overlying and underlying limestone beds.



The average thickness of the Hungry Hollow Formation is c. 2.0 m in the immediate study area. This formation consists of a highly fossiliferous calcareous shale bed 1.1 m in thickness which is bounded stratigraphically above and below by less fossiliferous grey limestone beds, .4 m and .5 m in thickness respectively (Plates 1-4). The coral-rich shale beds are laterally extensive and are readily recognizable in the outcrops of the area. There are very sharp contacts between the shale and the overlying and underlying limestones. The limestone can be classified (Folk, 1962) as a biomicrite. The calcareous shale is densely packed with numerous species of fossils and fossil fragments bound together by the grey shale (Plate 5). The most abundant fauna are solitary rugose corals, tabulate head corals, bryozoans, disarticulated crinoid ossicles and trilobite skeletal fragments (Table 1).

The fossils are very well preserved, poorly sorted and show relatively little abrasion. The rugose corals are found lying on their sides (ie. not in life position) within the shale beds and have their long axes orientated in a general east-west direction. Tabulate coral heads are found both in life position and overturned. The overwhelming majority of the corals are found within the shale beds along with the other fossil types listed in Table 1. The limestone beds are much less fossiliferous but do contain very few rugose corals, trilobites and brachiopods.

Plate 5: Hand sample of the coral zone of the Hungry Hollow Formation showing the high fossil content of bryozoans, crinoid ossicles and rugosa.



Table 1: Faunal List of the Major Fossils of the Hungry Hollow Formation

Rugose Corals: Cystiphyllum superbum
Eridophyllum archiaci
Heliophyllum halli
Zaphrentis prolifera

Tabulate Corals: Favosites sp.
Aulopora sp.
Alveolites sp.

Brachiopods: Mucrospirifer thedfordensis
Mucrospirifer arkonensis
Rhipidomella penelope
Callipleura nobilis

Trilobite: Phacops rana

Bryozoans: Fenestrellina sp.
Other encrusting Cheilostomata, trepostomata
and Cyclostomata

Crinoids: disarticulated ossicles

Chapter 2 - Growth Line Analysis of Heliophyllum halli

2.1 Introduction

The epitheca of well preserved, solitary rugose corals is characterized by external growth lines. These growth lines are defined as "abrupt or repetitive changes in the character of an accreting tissue" (Clark, 1974). Wells (1963), Scrutton (1965) and others recognized the occurrence of periodicities of these growth lines. These periodicities are the result of patterns of environmental stimuli that affect the corals during their ontogeny. Patterns of stimuli can be subdivided into random and periodic. Growth lines caused by random events are referred to as disturbance lines while those created by periodic events are called periodic lines. Disturbance lines caused by environmental events would be recorded on numerous members of the living coral population. These disturbance lines should be correlative among individuals of the coral population. In contrast, periodic lines would be recorded on all members of the population.

2.2 Previous Work

Wells (1963) considered the fine growth ridges to represent diurnal increments of growth. Working on Devonian

corals, he counted the growth ridges for annual growth cycles and found that there were approximately 400 growth ridges per year. He found that this value is consistent with astronomical calculations. This evidence suggested that the fine growth ridges on coral epithecae represented diurnal increments of calcium carbonate deposition. Wells also noted other growth cycles that were suggestive of a monthly periodicity. Counts of fine growth increments made on modern corals (Manicina areolata) by Wells resulted in a mean value of 360 which added supportive evidence to the work done on the Devonian corals. Paleontological and astronomical evidence indicate a progressive reduction in the number of days per year throughout geologic time due to a reduction in the Earth's rotational rate.

Scrutton (1965) also worked on growth increments in corals. He investigated the growth increments on Devonian corals in an attempt to test the results obtained by Wells (1963). The specimens he used did not display the same annual growth bands but displayed bands more indicative of monthly growth. For the fine ridges, Scrutton obtained an average of 30.5 deposited per band and 13 bands per Devonian year. These results agreed well with data obtained by Wells (1963) and astronomical calculations for the number of days in a Devonian year. The hypothesis favoured by Scrutton is that the fine growth lines represent solar days and the monthly bands are the result of breeding periodicities in

lunar months.

Barnes (1972) presented further experimental evidence for modern M. areolata to confirm the hypothesis of Wells that the fine growth ridges represent daily carbonate deposition. He noted that the growth ridges on the epithecae of M. areolata were produced by daily changes in the shape of the epithelial tissues secreting the skeleton. The daily increments are probably produced by the solar light-dark cycle as the result of the coral-algal symbiosis.

2.3 The Epitheca

Well preserved specimens have a complete epitheca while others have one side or two opposing sides that are poorly preserved. In some specimens, the epitheca has been completely worn away on one side. These sides correspond to those parts of the prone corallite that are in direct contact with the underlying sediment or overlying sediment of the coral zone in the Hungry Hollow Formation (Plate 6). This may be a diagenetic effect caused by pressure exerted by the rock overburden or percolating ground waters that have acted to dissolve portions of the epithecae. The coral epithecae may have been partially removed after death but prior to deposition within the Hungry Hollow Formation. The solitary coral specimens all show various, well developed ridges and bands that encircle the epitheca.

The successive ridges display variation in width and

Plate 6: Corallite whose epitheca has been partially removed. The narrow ridges extending the length of the corallite are septa.

Heliophyllum halli



relief. Wells (1963) and Scrutton (1965) showed that these ridges were formed by the incremental growth of the coral. Three magnitudes of growth increments are visible. Fine ridges barely visible with the unaided eye are referred to as growth cycle I (Plates 7-10). These are grouped into wider bands that are readily visible and these are designated as growth cycle II (Plates 9-13). These bands are grouped further into larger scale periodicities which are called growth cycle III (Plate 11 and fig. 4). Portions of the epithecae are defined by large constrictions. It is shown below that no clear periodicity is obvious for these sections. These portions are referred to as segments.

The epithecae also reflect environmental disturbances that affected the polyp during growth and these are possibly presented as various constrictions, rejuvenescence, geniculation and variations in the size and occurrence of growth ridges. The occurrence of numerous types of epizoans is very prevalent on the epithecae.

2.4 Material and Measurement Techniques

All measurements (Fig. 4) were made on the solitary rugose Heliophyllum halli (Edwards) in order to avoid variations due to taxonomic differences. The growth increments were measured with the use of a Vernier scale and dividers. Cycle I counts were done under a binocular dissecting microscope. The corallite diameter for each

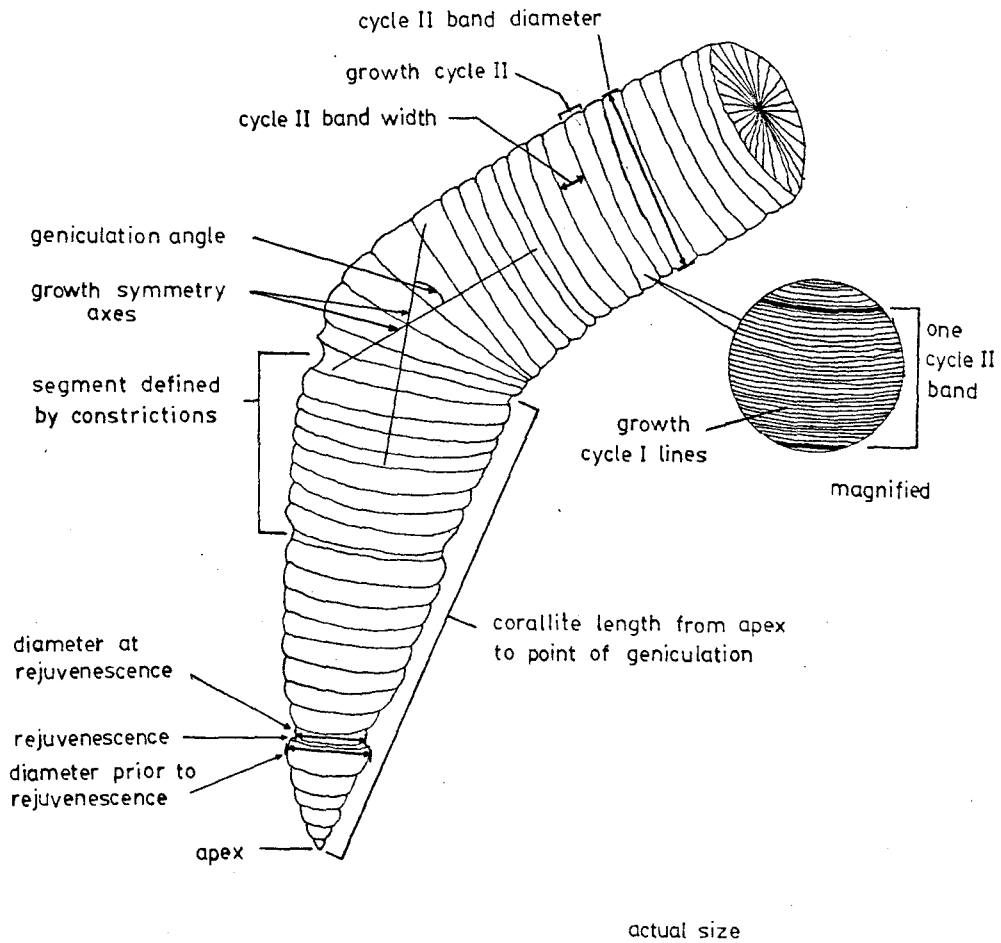


Fig.4 IDEALIZED RUGOSE CORAL ILLUSTRATING THE VARIOUS PARAMETERS

Plate 7: Cycle II (monthly) bands (M) each with approximately 30 Cycle I (daily) lines.
Heliophyllum halli
Scale in cm.

Plate 8: Corallite epitheca with Cycle I (daily) growth lines and aggregates of hematite rosettes (h).
Scale in cm.
Heliophyllum halli



Plate 9: A Cycle II (monthly) band showing the fine
Cycle I (daily) growth lines.

Scale in cm.

Heliophyllum halli

Plate 10: Well preserved Cycle I (daily) growth lines
within Cycle II (monthly) bands.

Scale in cm.

Heliophyllum halli

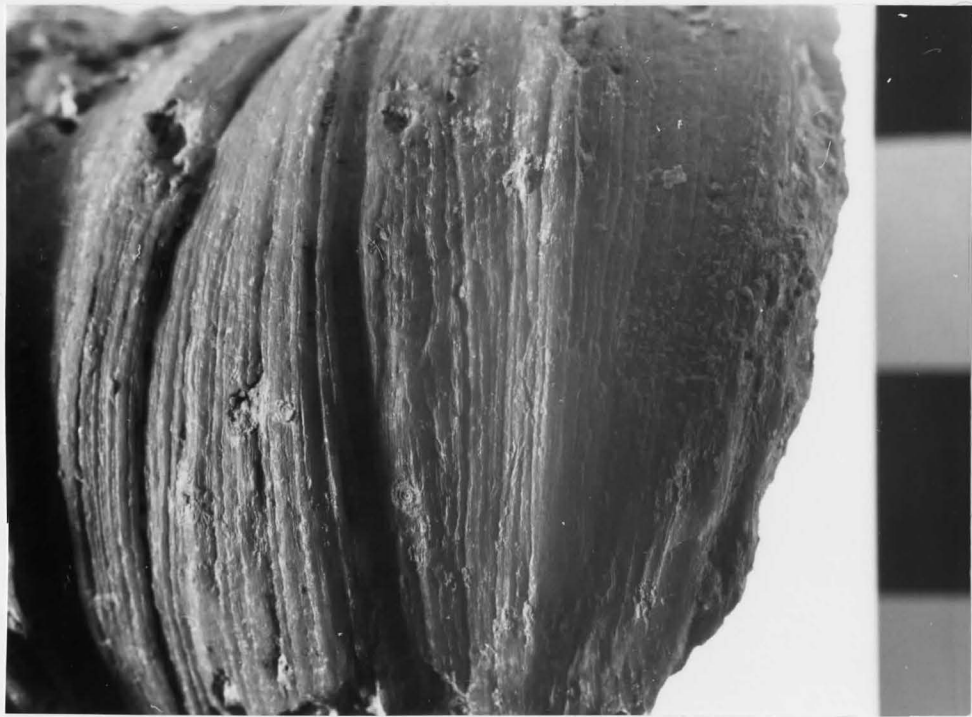
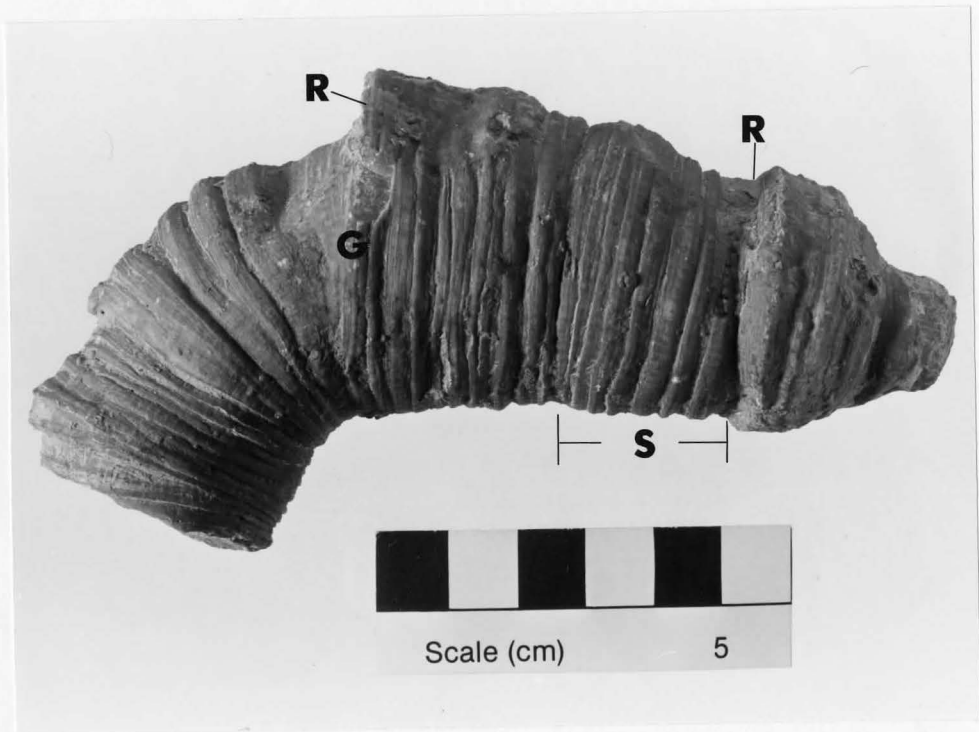


Plate 11: Corallite showing well defined Cycle II (monthly) growth bands and two possible Cycle III (annual) cycles (A) of thirteen monthly bands. Also note the decreasing apical angle with ontogeny causing a change in corallite shape.
Heliophyllum halli

Plate 12: Corallite showing well defined Cycle II (monthly) bands and rejuvenescence (R) associated with geniculation (G). Segments (S) are defined by epithelial constrictions.
Heliophyllum halli



cycle II band was measured using the Vernier scale. The widths of these bands were measured between consecutive constrictions which define these bands. Only a few measurements were made for cycle III due to the few well-defined occurrences.

The sections of the epithecae bounded by constrictions were measured in the same manner as the three growth cycles. Large constrictions caused by periods of rejuvenescence were measured to obtain the average difference in corallite diameter between the constriction and the adapically adjacent portion of the epitheca. Angular measures of geniculation were obtained between the estimated symmetry axes before and after geniculation.

Consistent methods and techniques of measurement were employed to minimize the experimental errors. Numerous measurements were made at different points on the coral epithecae for each measurement and a mean value was recorded. These mean values and a large number of measurements reduced the effects of epithecal irregularities. A certain amount of experimental error was invoked by irregular surfaces of the coral epithecae, slightly flattened corals, poorly defined growth lines or bands, irregular growth lines, poorly defined constrictions, curved coral skeletons and periods of geniculation and rejuvenescence. Careful observation to discern boundaries and lines probably reduced measurement errors to a minimum.

Growth cycle measurements were made on corals with a relatively undisturbed ontogeny. Measurements on geniculate corals were made only adapically to the point of geniculation. Many of the specimens were without an apex but for the purpose of measurements an extrapolation of the conical shape was performed to ascertain the approximate apical position. An uncertain amount of error may have been created in the measurements of the geniculation angle by estimating the symmetry axes but this was the only practical measure.

The corals may also have had growth irregularities that caused them to omit one or several daily growth increments. Other environmental irregularities may have created an increase or decrease in the growth rates of some corals within the population but there is no way of correcting for such irregularities.

2.5 Growth Cycle I

The growth line counts (fig. 5) show that there is a mean of 30.38 cycle I lines per cycle II band (Plates 7-10). The actual counts range between 28 and 34 lines per band. Counting errors due to discontinuous and obscured lines may have been responsible for this range. The record of growth cycle I may be slightly irregular due to the omission of a line at one time or the deposition of more than one line at other times.

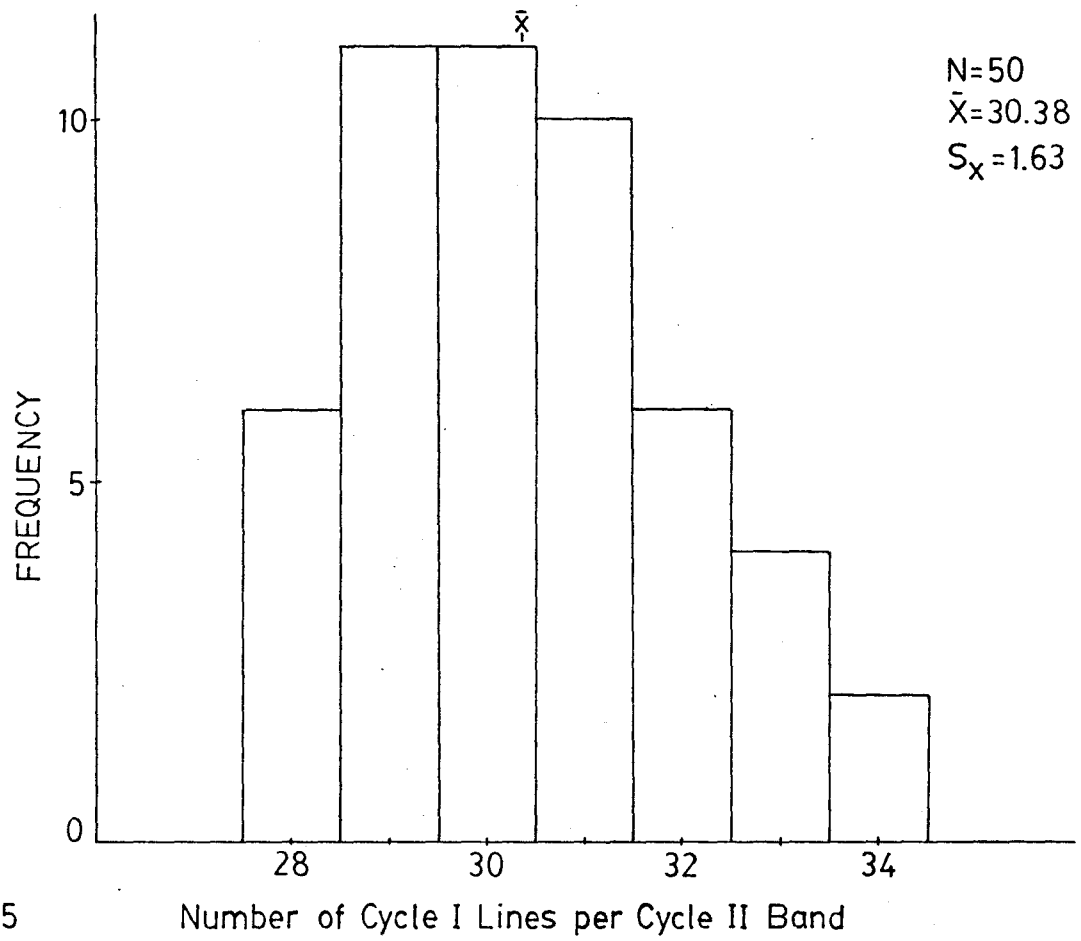


Fig.5

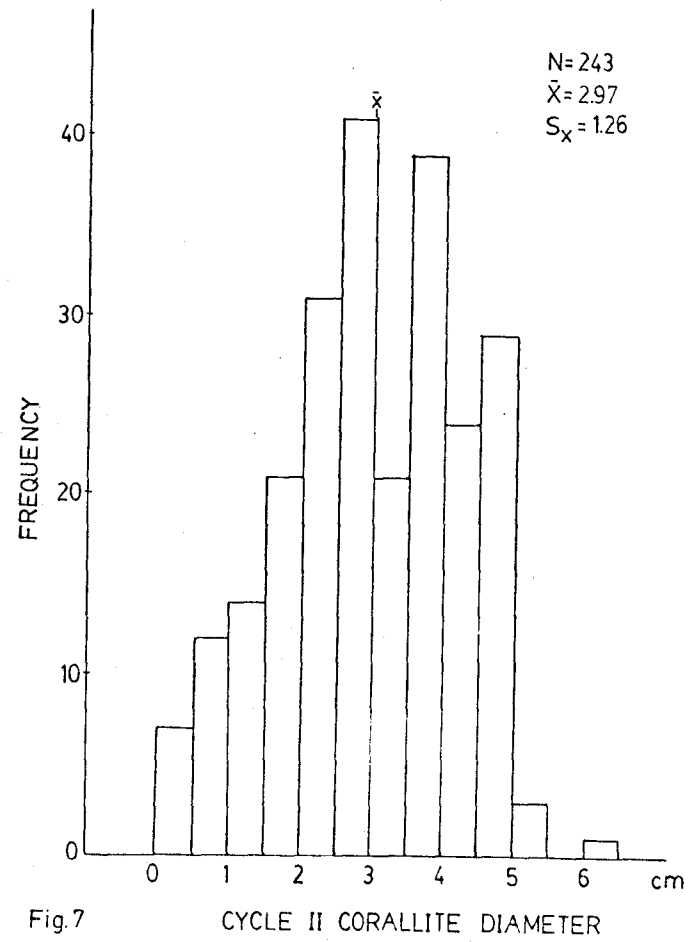
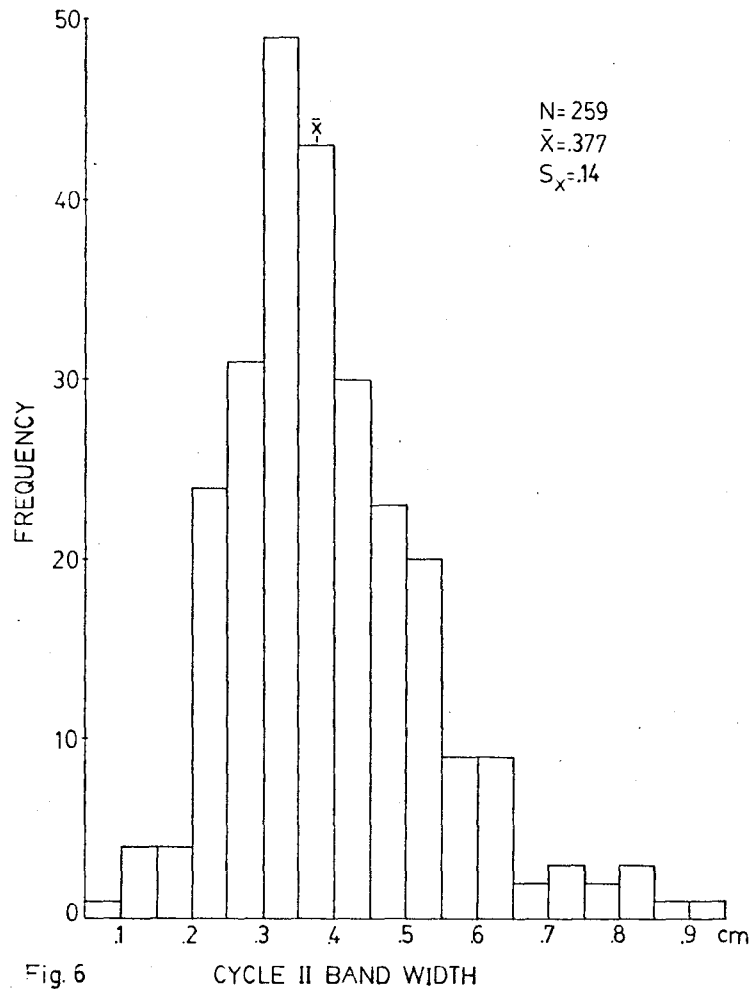
Number of Cycle I Lines per Cycle II Band

2.6 Growth Cycle II

The measurements of 259 cycle II bands resulted in a mean width of .377 cm. The distribution of widths (fig. 6) is such that 84.9% of the bands have widths between .2 and .55 cm. The histogram illustrates occurrences of a few band widths less than .2 cm (about 3.5%) and a somewhat greater frequency of band widths greater than .55 cm (11.6%).

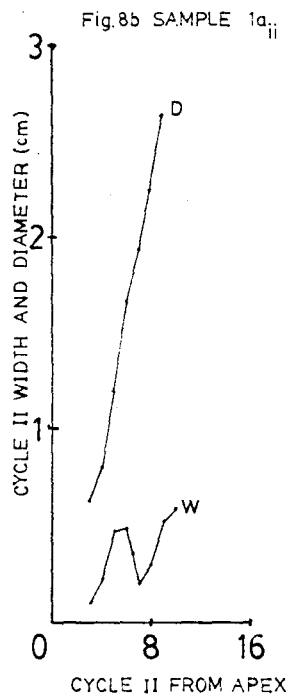
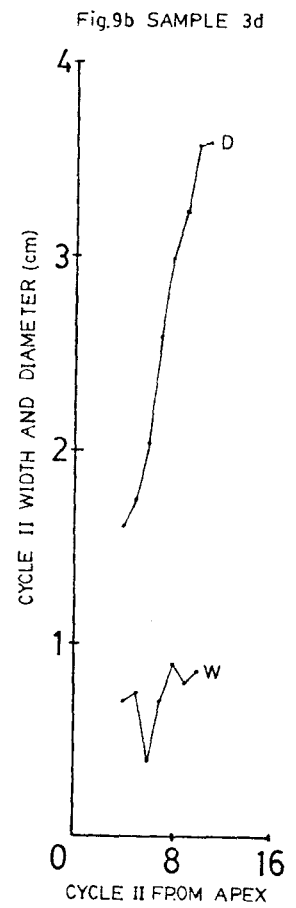
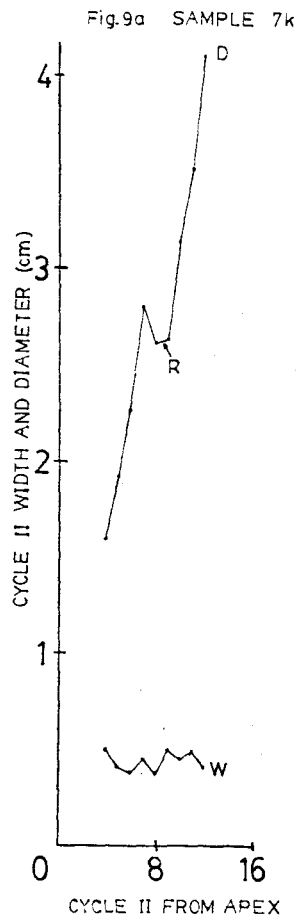
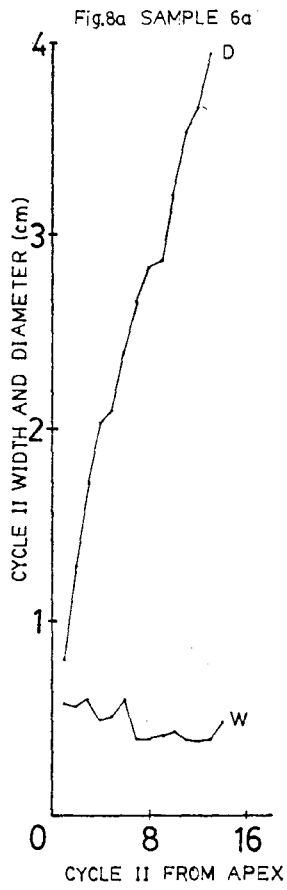
Measurements of corallite diameter made at 243 cycle II bands (fig. 7) have a mean of 2.97 cm. The histogram distribution of figure 7 also reflects the general growth characteristics of the corallite. During the early portion of the ontogeny the corallite increased isometrically in diameter to produce a cone (Plate 11, 13). At approximately 3.0 cm diameter the growth became slightly irregular and anisometric resulting in a change of corallite shape to cylindrical. A precise graphical representation of this anisometry will be discussed in a subsequent section. The other feature of figure 7 is the lack of corallite diameters greater than 5.0 cm. This is a general characteristic of the corallite population sampled from the Hungry Hollow Formation.

Diameter and width of the cycle II bands were plotted against bands from the apex for a few specimens (figs. 8-17). The number of bands from the apex is representative of time. Some fluctuations of diameter occur throughout the ontogeny of the corals and these are



reflected as decreases in the slope of the diameter lines. Some specimens (7k, 7o, 7r, 9j, 11d, 11f, 11x) show an interval of diameter decrease followed by an increase. These intervals represent periods of rejuvenescence during the growth of the coral. The general trend is increasing corallite diameter with time. In contrast, the width values seem to show no general trend during the ontogeny of the corals. The plotted width values are very irregular. There seems to be an apparent correlative decrease in width of the cycle II bands at approximately the seventh band from the apex. In a few specimens this decrease occurs at six or eight bands from the estimated apex but this may be attributed to estimation errors for specimens where apices were not complete. There is a less frequent occurrence of a decrease in band width at approximately fourteen bands from the apex (Specimens 7p, 7r).

The relationship between band width and the corallite diameter and time is not well defined (figs. 8-17). At certain times both width and diameter of the cycle II bands increase or decrease but other bands demonstrate an inverse relationship between width and diameter. There seems to be no consistent overall correlation or periodicity between the two parameters. The specimens do illustrate a general growth characteristic of the corals. Width and diameter increase strongly in the juvenile stage but the growth slows with age.



Figures 8-17: Cycle II Band Width and Diameter vs. Number of Cycle II Band from the Apex.

Fig.10a SAMPLE 7o

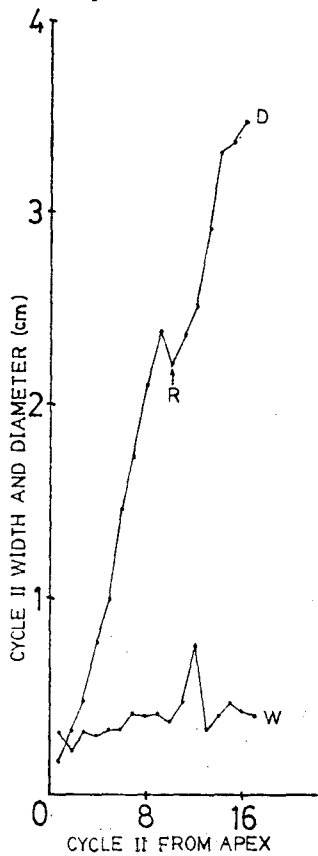


Fig.10b SAMPLE 3e

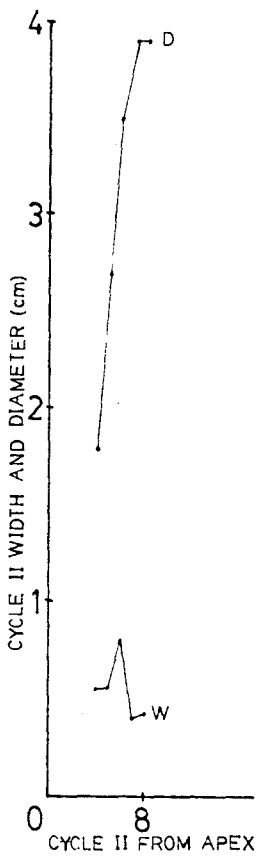


Fig.11a SAMPLE 3o

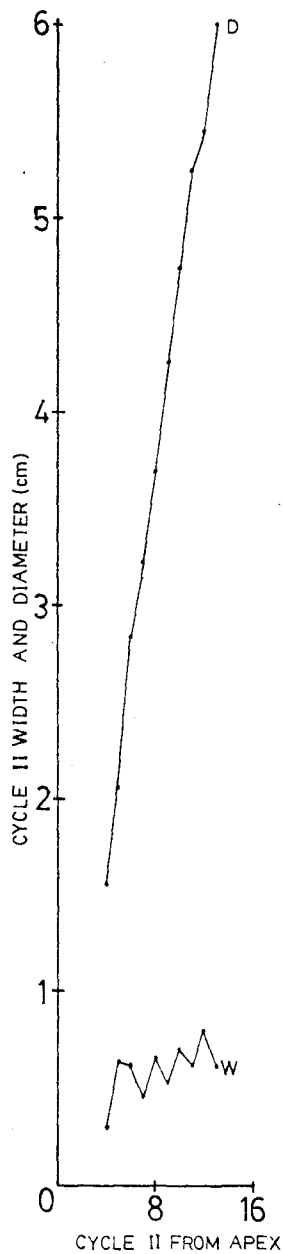


Fig.11b SAMPLE 7d

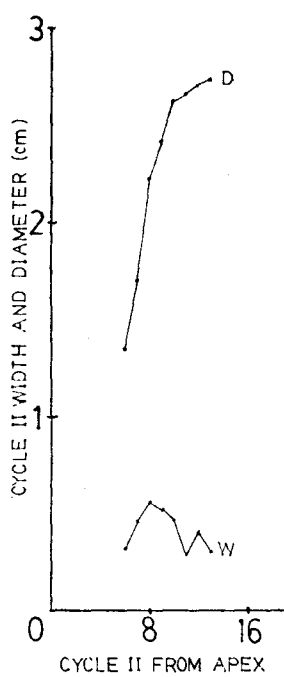


Fig. 12a SAMPLE 7p

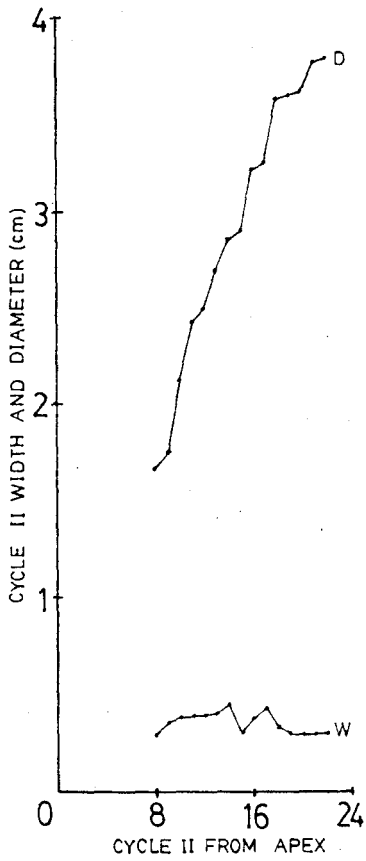


Fig. 12b SAMPLE 7r

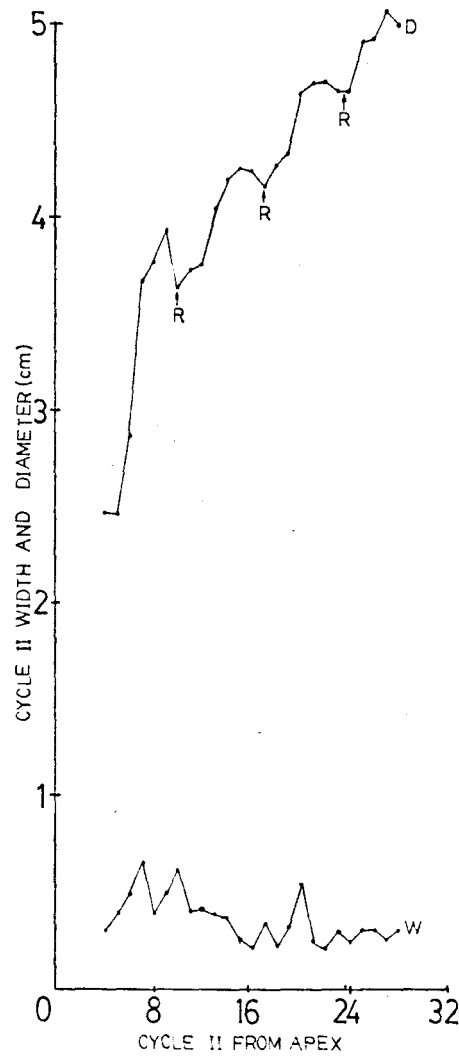
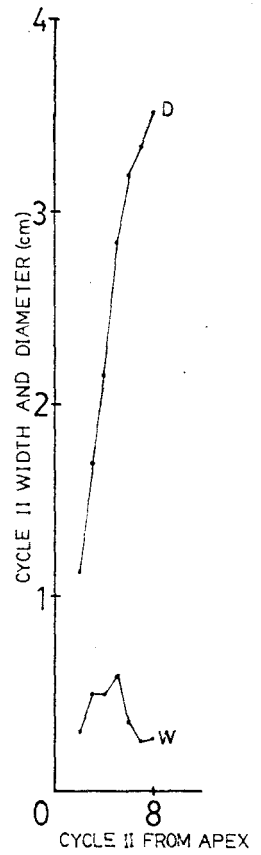
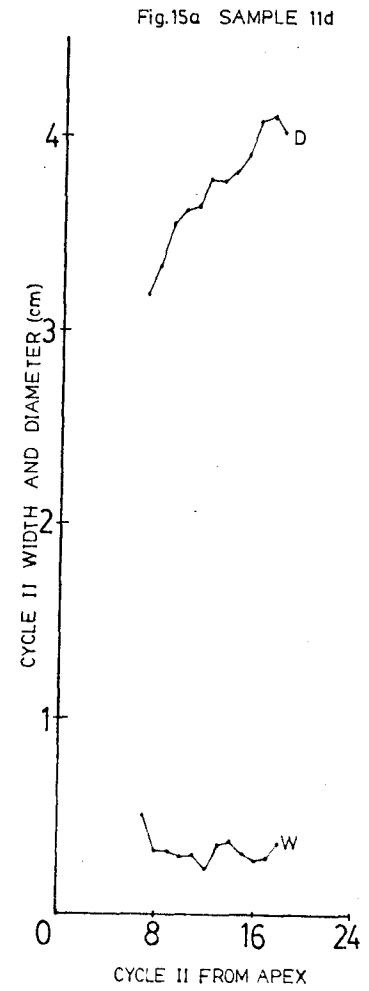
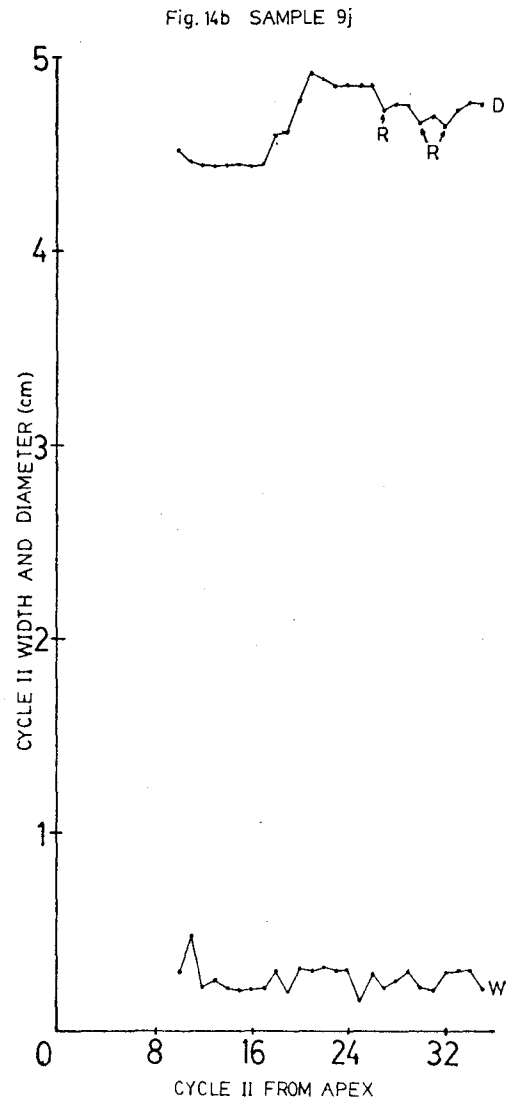
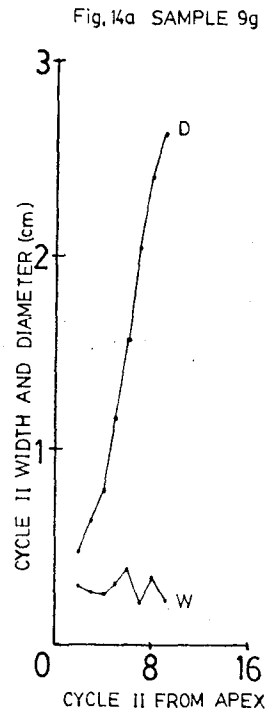
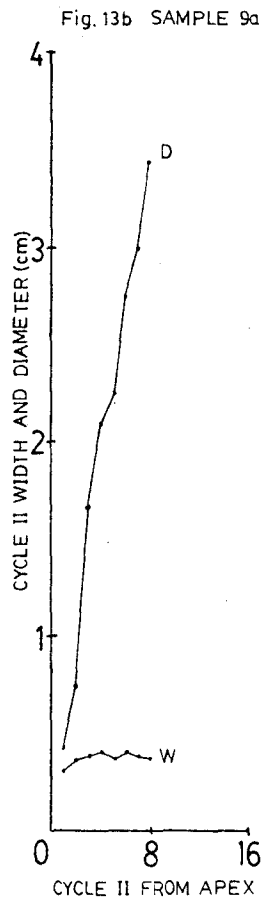


Fig. 13a SAMPLE 8a





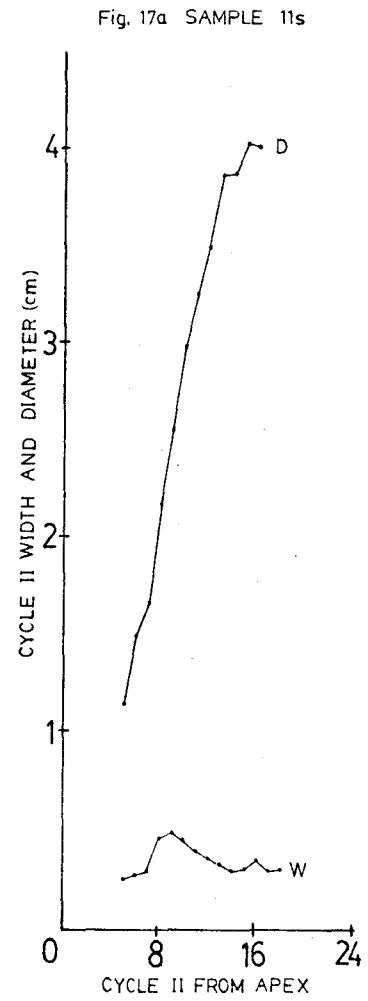
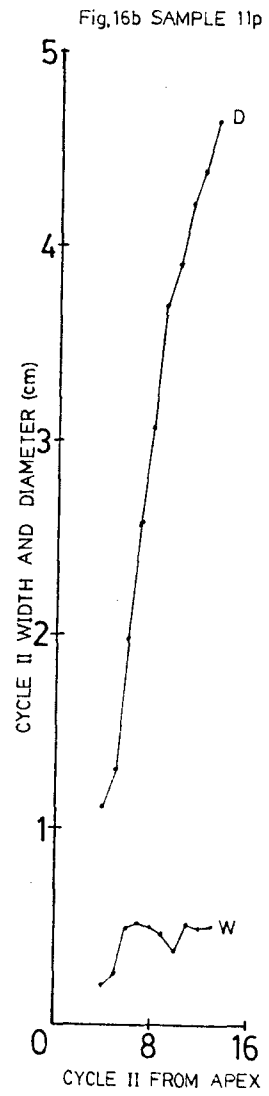
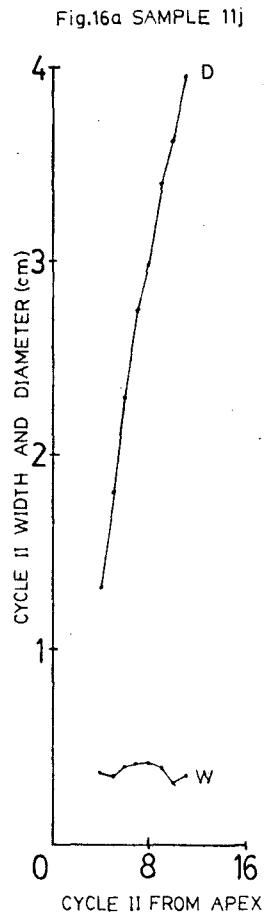
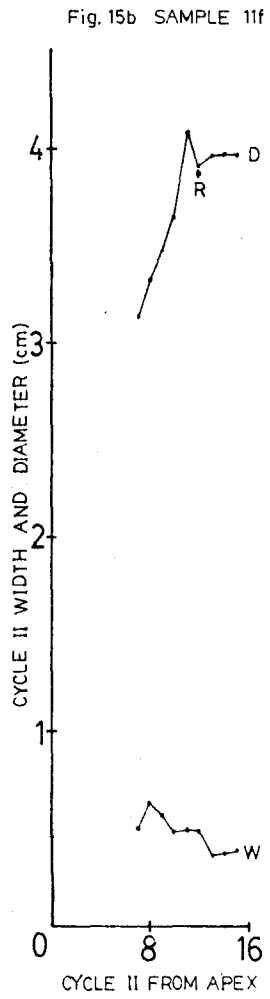


Fig.17b SAMPLE 11x

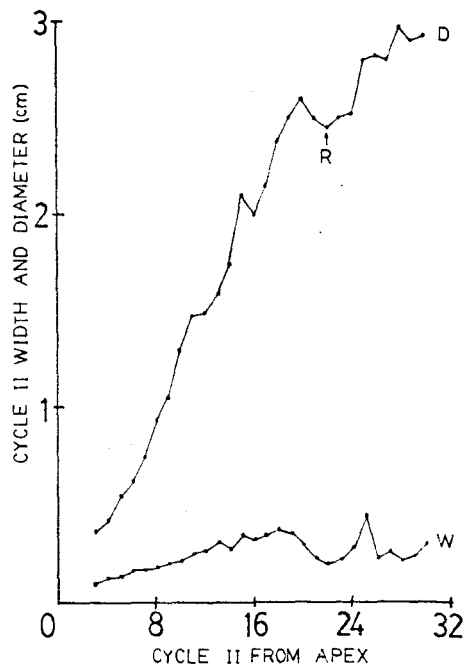


Fig.18a SAMPLE 3d

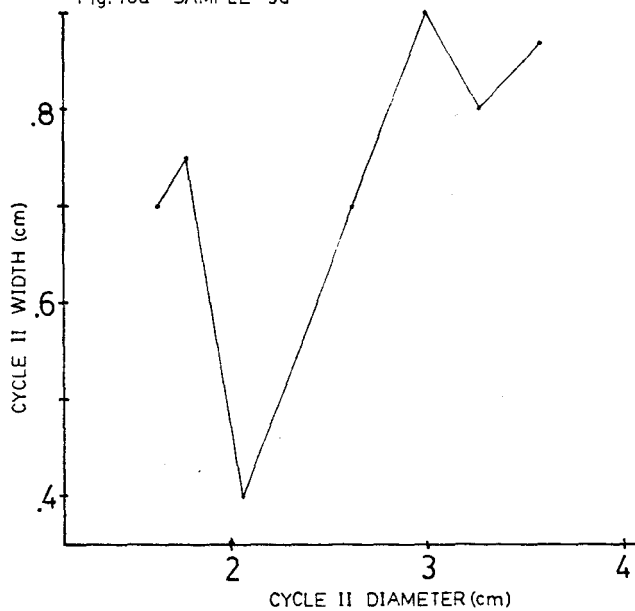


Fig.18b SAMPLE 3e

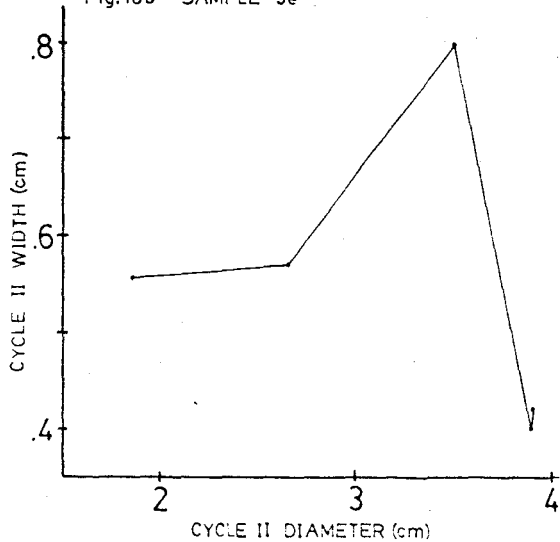
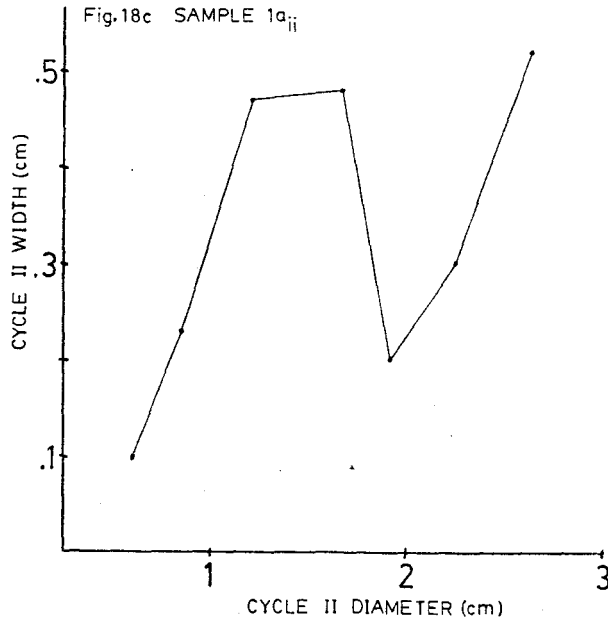


Fig.18c SAMPLE 1a_{ii}



Figures 18-25: Cycle II Band Width vs. Cycle II Diameter

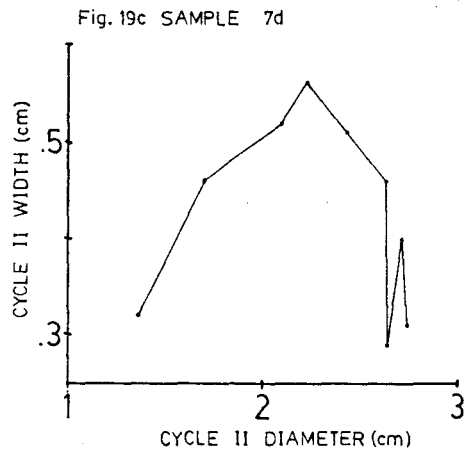
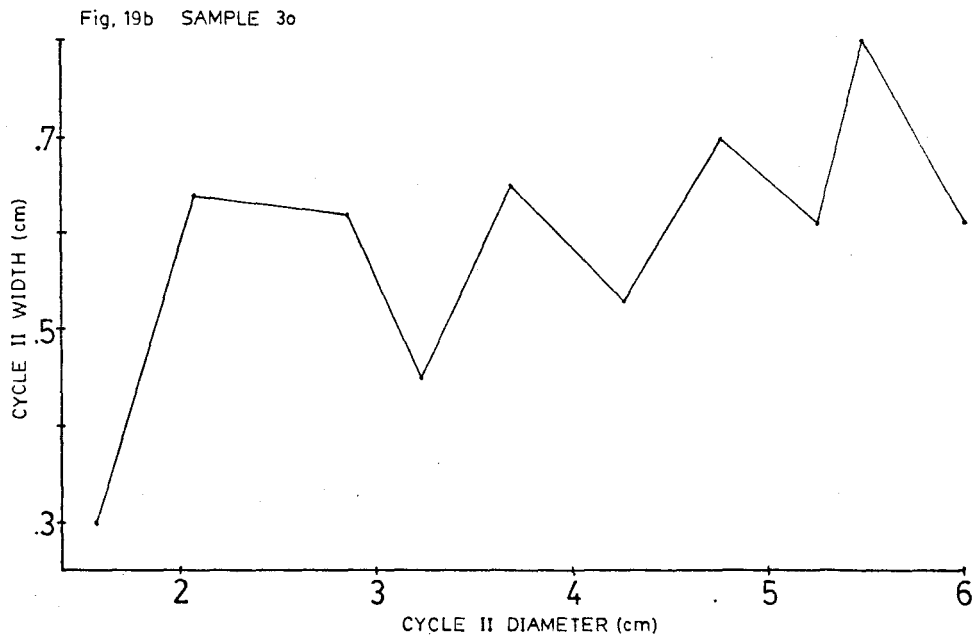
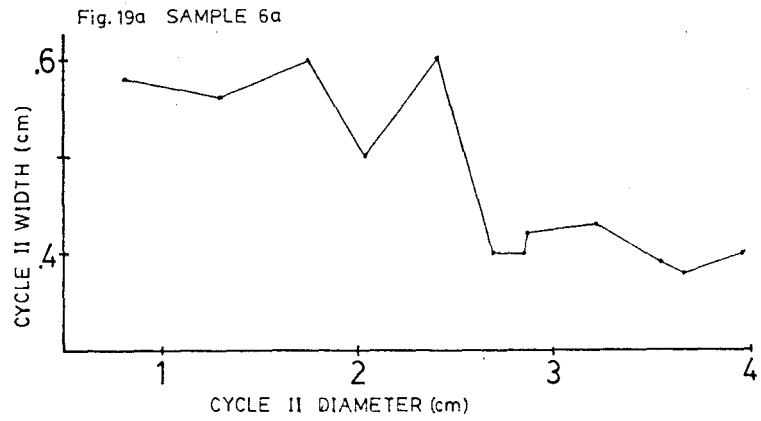


Fig. 20a SAMPLE 7o

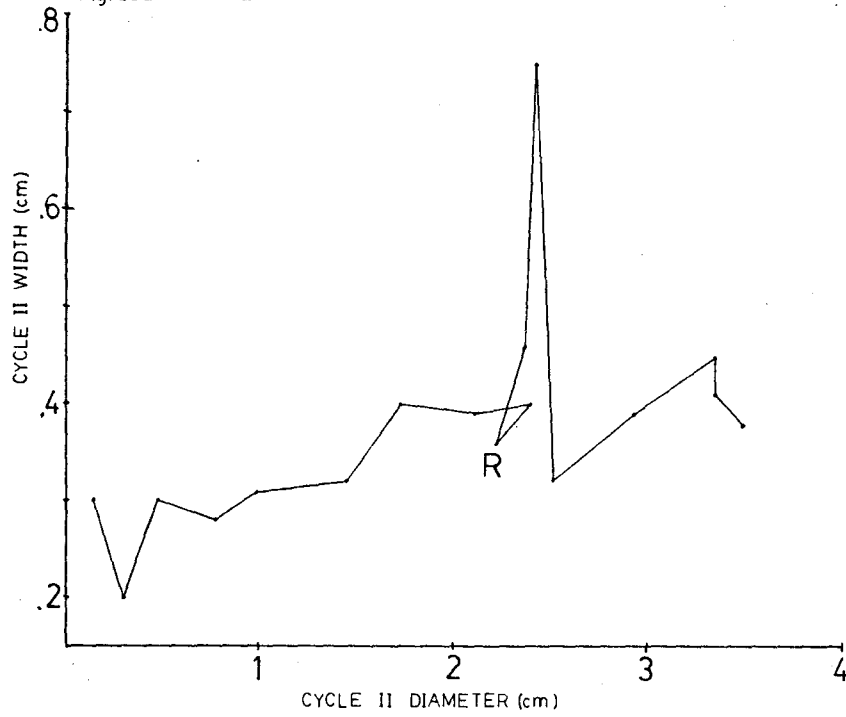


Fig. 21a SAMPLE 7r

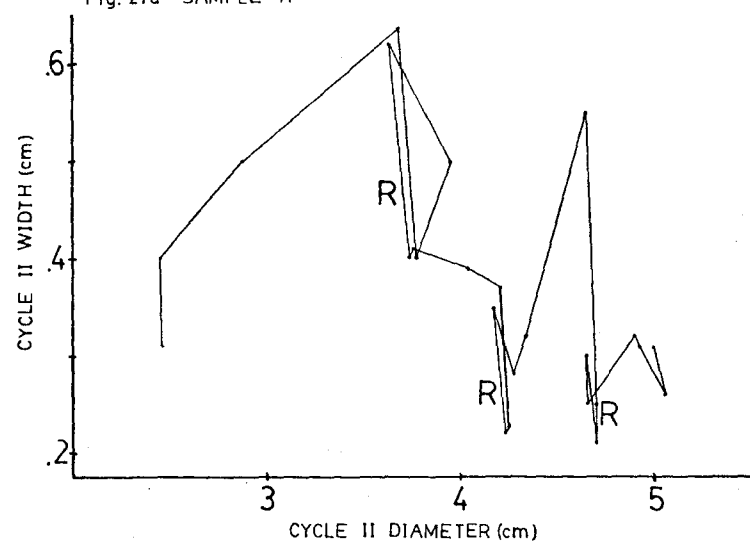


Fig. 20b SAMPLE 7k

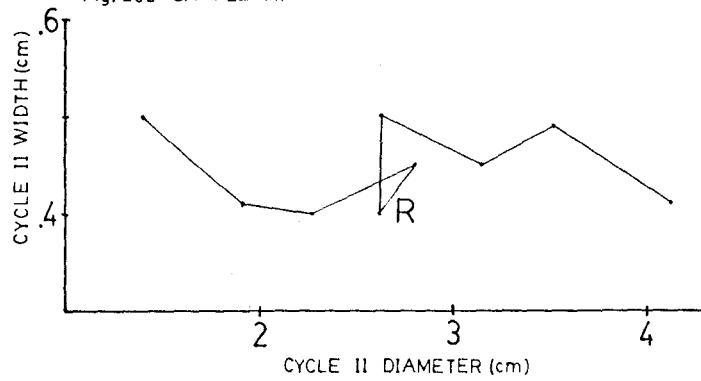


Fig. 21b SAMPLE 7p

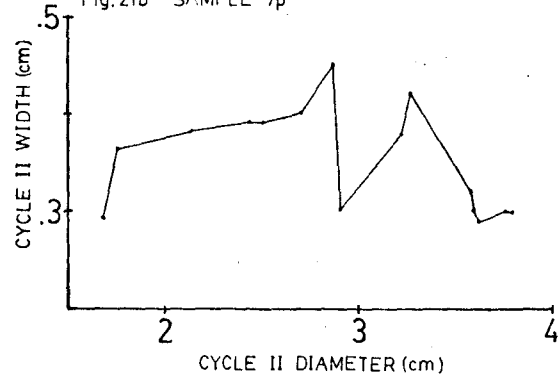


Fig. 22a SAMPLE 9a

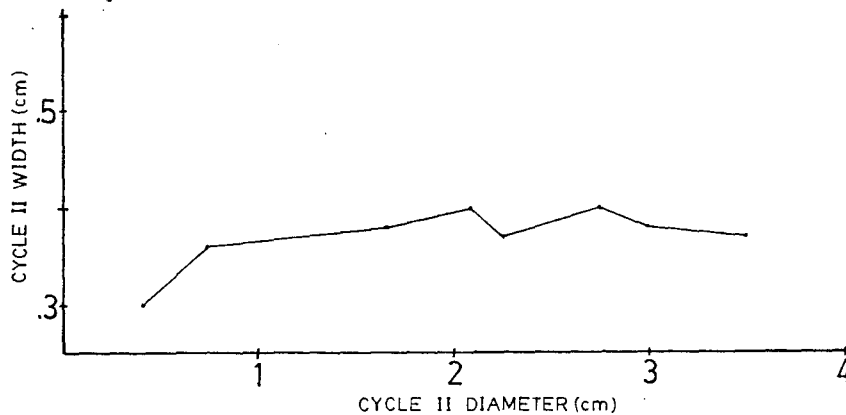


Fig. 22b SAMPLE 8a

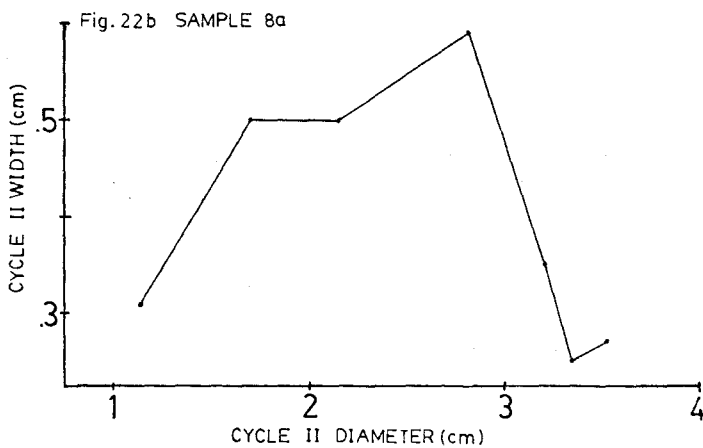


Fig. 22c SAMPLE 11d

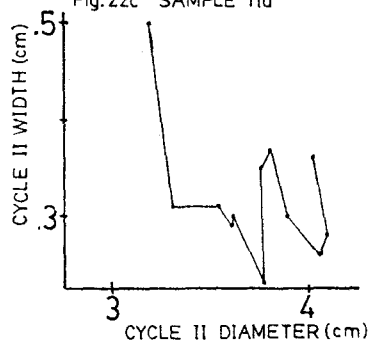


Fig. 23a SAMPLE 11j

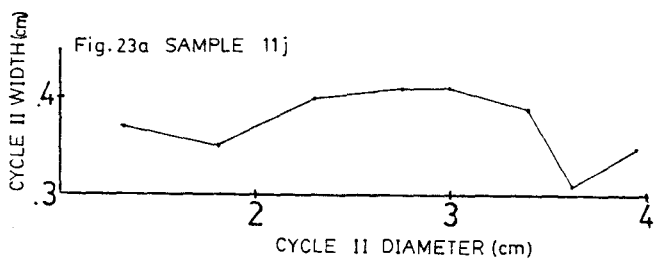


Fig. 23c SAMPLE 11f

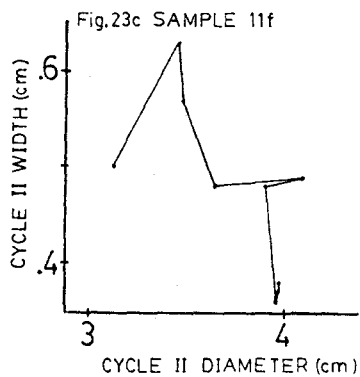
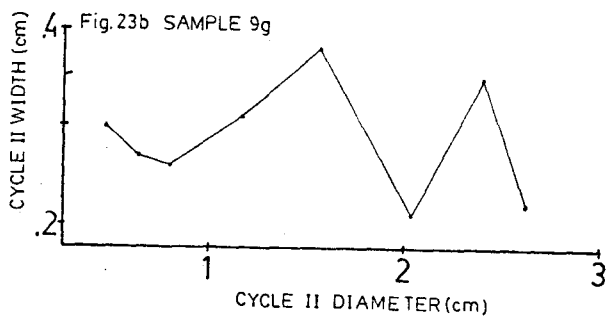
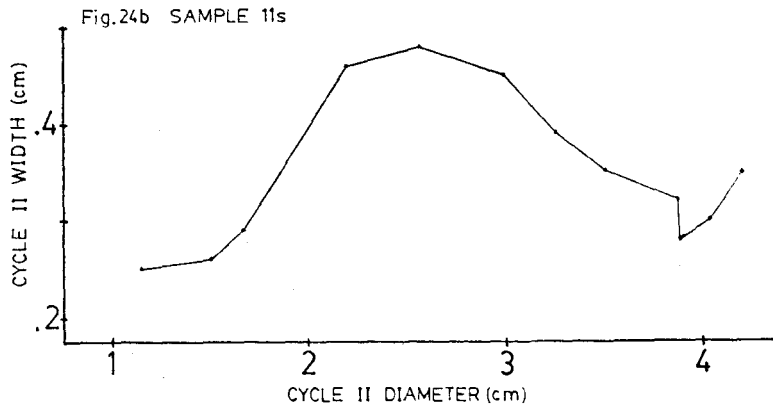
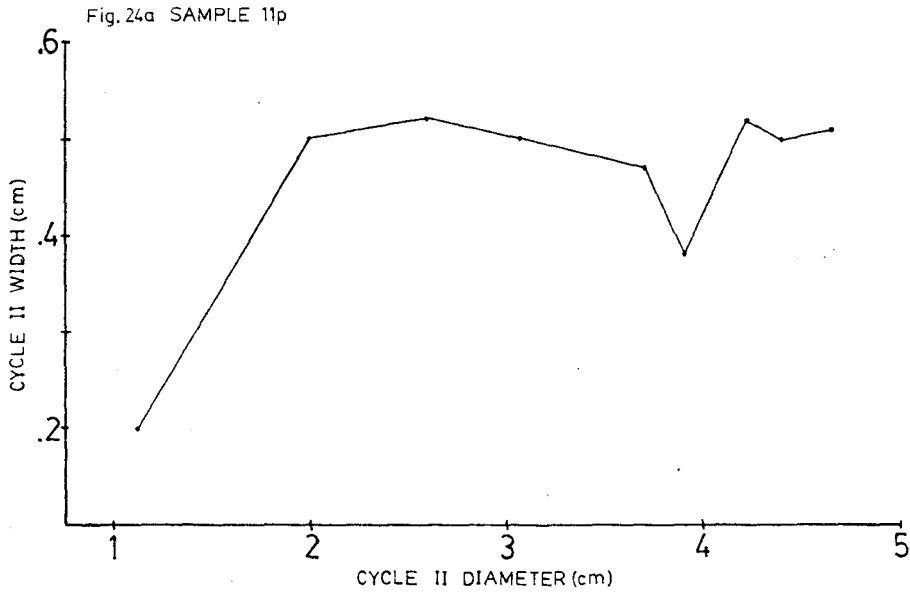
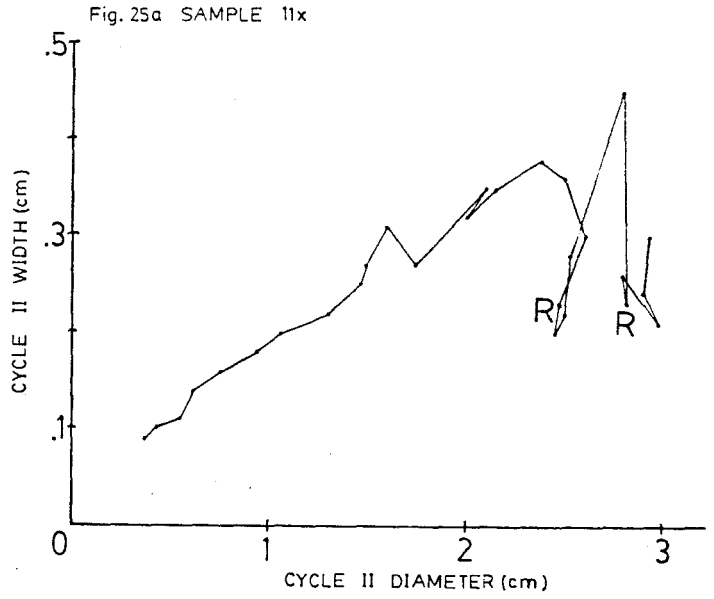
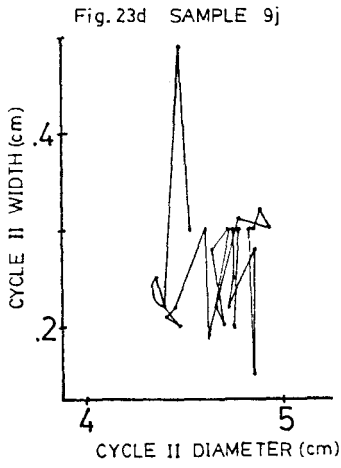


Fig. 23b SAMPLE 9g





Width of the cycle II bands was plotted against diameter (figs. 18-25). The graphs of the individual specimens show no overall trend between width and diameter and the lines of the graphs (figs. 18-25) have a zig-zag form. Plots of some specimens (7o, 7r, 7k, 9j, 11x) overlap an older portion of their growth. This is indicative of a period of rejuvenescence in which the diameter is reduced briefly during the growth history of the coral.

A scatter diagram (fig. 26) of width and diameter for the cycle II bands shows no obvious grouping of points. A linear regression produced the line $y = .0088 x + .35$ as shown in figure 26. A correlation coefficient of .0785 was calculated for the width and diameter values. Such a small value close to zero indicates a very poor linear correlation between width and diameter. This complies with the graphical evidence previously mentioned for the lack of any relationship between these two parameters.

2.7 Growth Cycle III

Periodicity or grouping is not well developed in the cycle II bands, except for a few specimens (9j, 7r, 11x, 15a). These periodicities are bounded by epithelial grooves and swellings and reductions of corallite diameter between these grooves (Plate 11). These slight variations of corallite diameter are probably due to seasonal temperature fluctuations (Wells, 1963 and Scrutton, 1965). The swelling

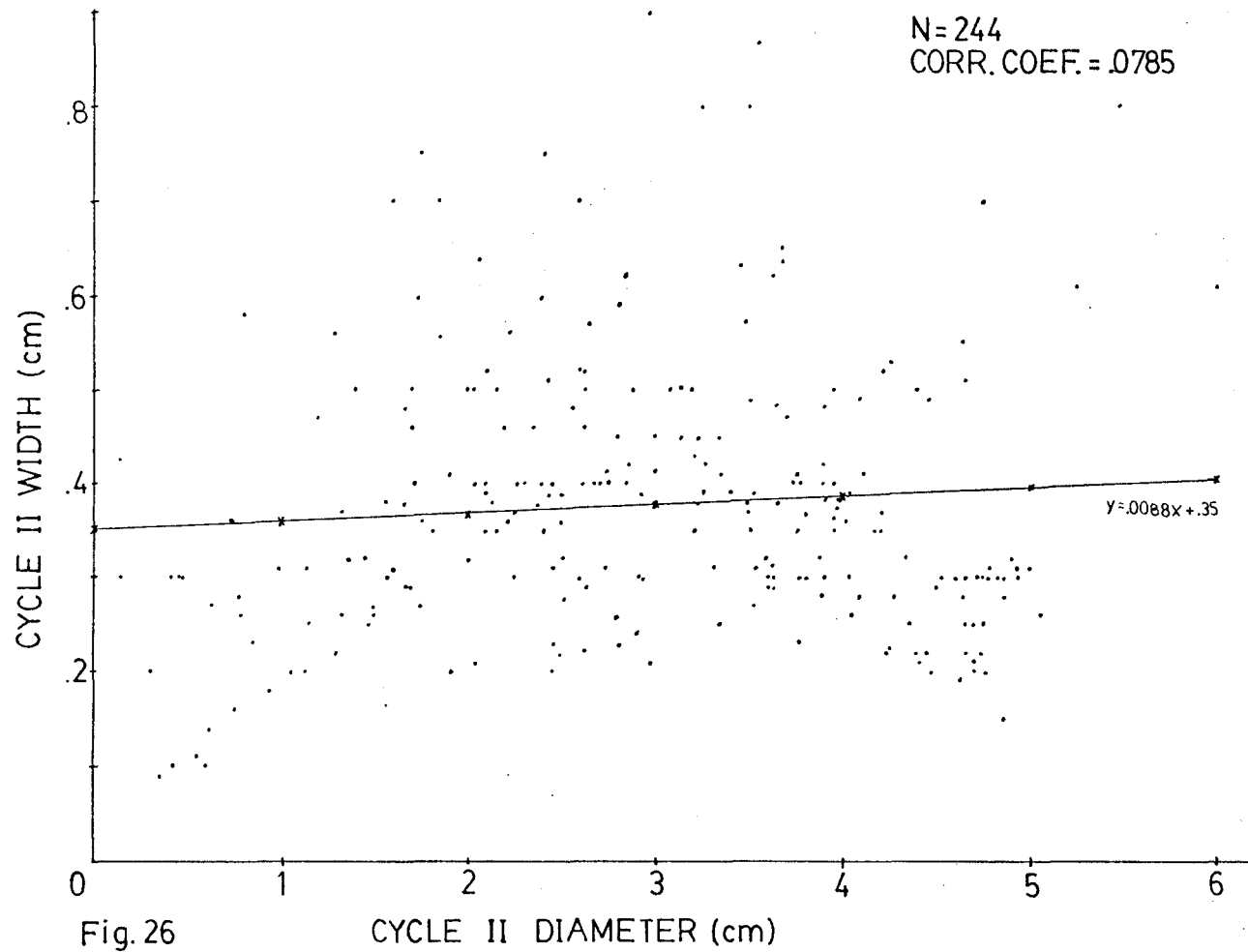


Fig. 26: Scatter Diagram of Cycle II Band Width vs. Cycle II Band Diameter.

corresponds to warmer summer temperatures which would facilitate the growth of the coral and the production of calcium carbonate. Cooler winter temperatures would have the opposite effect. Table 2 gives the approximate growth (vertical) of the coral for each possible cycle III periodicity recognized in a few specimens. The mean length is 4.29 cm.

2.8 Growth Cycle Discussion

a) Growth Cycle I

The mean of 30.38 growth lines per cycle II band corresponds closely to the value of 30.59 obtained by Scrutton (1965). Scrutton proposed that these lines represent daily calcium carbonate deposition by the epithelial tissues. The lines represent solar days as the result of increased calcium carbonate deposition during the day caused by increased metabolism of the coral due to the coral-symbiotic algal association. Subsequent work by Barnes (1972) on M. areolata presented observational evidence supporting this hypothesis. Thus the fine growth lines defined as growth cycle I can be regarded as daily growth increments.

b) Growth Cycle II

The mean of 30.38 for daily growth lines implies the monthly cyclicity of these bands as previously proposed by Scrutton (1965) and Wells (1963). The probable cause for

such a periodicity is a lunar breeding cycle of the corals as suggested by Scrutton (1965), although he does suggest other possible causes. The actual cause of such a cyclicity may be a combination of factors in addition to the breeding cycle such as tidal effects and nutrient supply as suggested by Scrutton. The monthly periodicity may be defined as a synodic month which is the time between consecutive new moons (Clark, 1974). It is thought that the illumination of the full moon may trigger spawning.

Assuming that a cycle II band represents monthly growth, their mean width of .377 cm equals the average monthly vertical growth of the corallite. The fact that 84.9% of the bands are between .20 cm and .55 cm in width indicates a relatively consistent monthly growth rate of the coral population. The monthly growth variations may be indicative of adverse or optimal growth conditions experienced by portions of the coral population.

Apart from a maximum mean corallite diameter of 2.97 cm, the histogram (fig. 7) illustrates a sharp decline in the frequency of corals with a diameter greater than 5.0 cm. The corallite apical angle of the cone decreases with age. This explains why even old corals rarely obtained a diameter greater than 5.0 cm.

Data for band width and corallite diameter indicate a very poor linear correlation between these two parameters. Band width (ie. monthly growth) seems to be independent of

the monthly growth rate in corallite diameter.

The general growth of the corals may be regarded as anisometric in which the ratio between the sizes of two parts of the corallite changes during ontogeny. This means that there is a change in shape. The parameters involved are monthly growth rate and corallite diameter. In the juvenile, the corallite diameter increases rapidly with respect to the monthly vertical growth thus producing a cone with a moderately large apical angle. The monthly rate of diameter increase slows (ie. negative growth rate) relative to monthly vertical growth with increasing age and thus the apical angle of the cone is reduced.

c) Growth Cycle III

The seasonal fluctuations, that are poorly developed as a pair of corallite expansion and contraction in the coral samples, may represent a yearly cycle. Wells (1963) and Scrutton (1965) determined that there were annual growth cycles. Sample 9j (Plate 11) shows thirteen monthly bands within poorly developed possible annual bands. Thirteen monthly bands each with 30.35 diurnal lines gives an approximation of 395 days per Middle Devonian year. Scrutton (1965) determined that there were thirteen monthly bands and four hundred daily lines per Middle Devonian year as recorded on rugose corals. The poorly developed annual cycles of the sample corals of the Hungry Hollow Formation do not convincingly contain thirteen monthly bands per year.

Table 2 shows the approximate annual growth increments for several specimens. Mean annual growth of these possible annual cycles is 4.29 cm. If the monthly mean growth of .377 cm is multiplied by thirteen months then an approximate annual growth rate for the corallites is 4.9 cm. Table 2 has only a limited number of values used in determining an annual growth rate. A larger sample population size may have provided an annual growth rate closer to that of the calculated value of 4.9 cm. An annual growth rate in corallite diameter cannot be determined due to the high variability in diameter and its negative growth rate relative to vertical growth and age.

The lack of a well developed periodicity in the seasonal Cycle III probably indicates that the corals of the Hungry Hollow Formation grew in an area relatively unaffected by seasonal fluctuations. Figure 27 shows the approximate position of the equator during the Middle Devonian and the study area at a latitude of approximately 33°S. This latitude probably experienced negligible seasonal fluctuations thus accounting for the lack of a well developed periodicity in the corals.

Table 2: Corallite Length (L) Increase per year

L (cm)

4.68
6.18
4.79
5.44
3.52
3.30
3.80
4.47
2.97
3.71

$N = 10$

Mean (\bar{X}) = 4.29 cm

$S_x = 1.01$

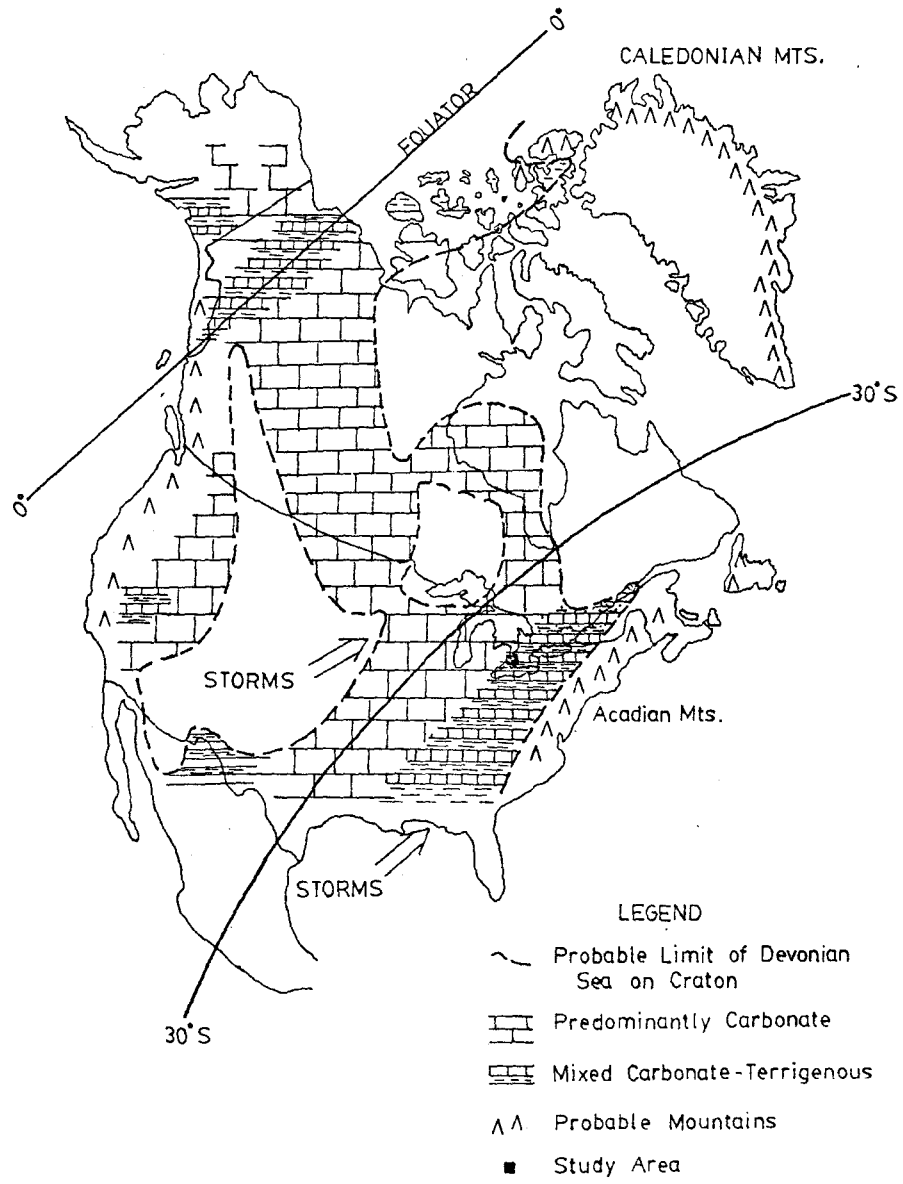


Fig.27 GENERALIZED MIDDLE DEVONIAN NORTH AMERICA

(After Scrutton, 1979)

Chapter 3 - Segments

3.1 Results

Measurements were made on the segments which were previously defined as portions of the epithecae bounded by large constrictions (fig. 4, Plate 12). A histogram of segment lengths and the mean are shown in figure 28. The average length is 2.24 cm. The corals often possessed more than one segment and each consecutive segment was numbered accordingly. Average length values for the segments are 2.42 cm, 2.04 cm, 2.19 cm and 2.38 cm for the first, second, third and fourth segments respectively. These values for the individual segments deviate little from the mean value of 2.24 cm obtained for all the segments collectively. A linear regression of the segments provides the equation of the line $y = .374 x + 1.49$. A correlation coefficient of .928 calculated for the segment diameter and length indicates a very high positive linear correlation.

The occurrences of the various segments define fields that are indicated in figure 29. Linear regressions for the individual segments and their corresponding fields of occurrence are shown in figure 30. The overall curvature defined by the points illustrates the general growth trend of the corallite. Differences in the diameter between

consecutive segments was investigated (Table 3). The average diameter increase from the apex to segment 1 is 2.36 cm, 1.21 cm from segment 1 to 2, .38 cm from segment 2 to segment 3 and .34 cm from segment 3 to segment 4. There is a significant increase in diameter between the first two segments but this diameter increase lessens significantly between subsequent segments as a function of time (coral age).

3.2 Discussion

Segment investigation illustrates the corallite growth trend of decreasing diameter growth rate relative to height with increasing age. This anisometric growth resulted in a change in the shape of the corallite during the ontogeny due to a decrease in the apical angle (Plates 11, 13). The coral grew rapidly until it achieved maturity at which time reproduction became more important and the growth rate slowed.

SEGMENT	1	2	3	4
N	24	25	17	11
\bar{X}	2.42	2.04	2.19	2.38
S_x	.76	.60	.72	.85

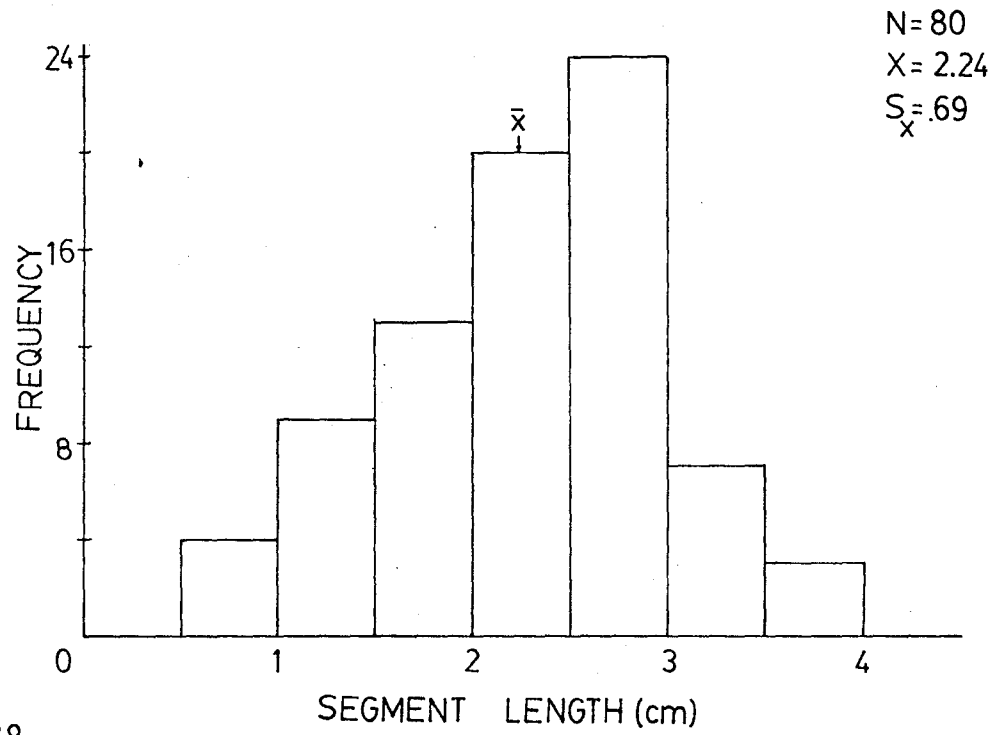


Fig. 28

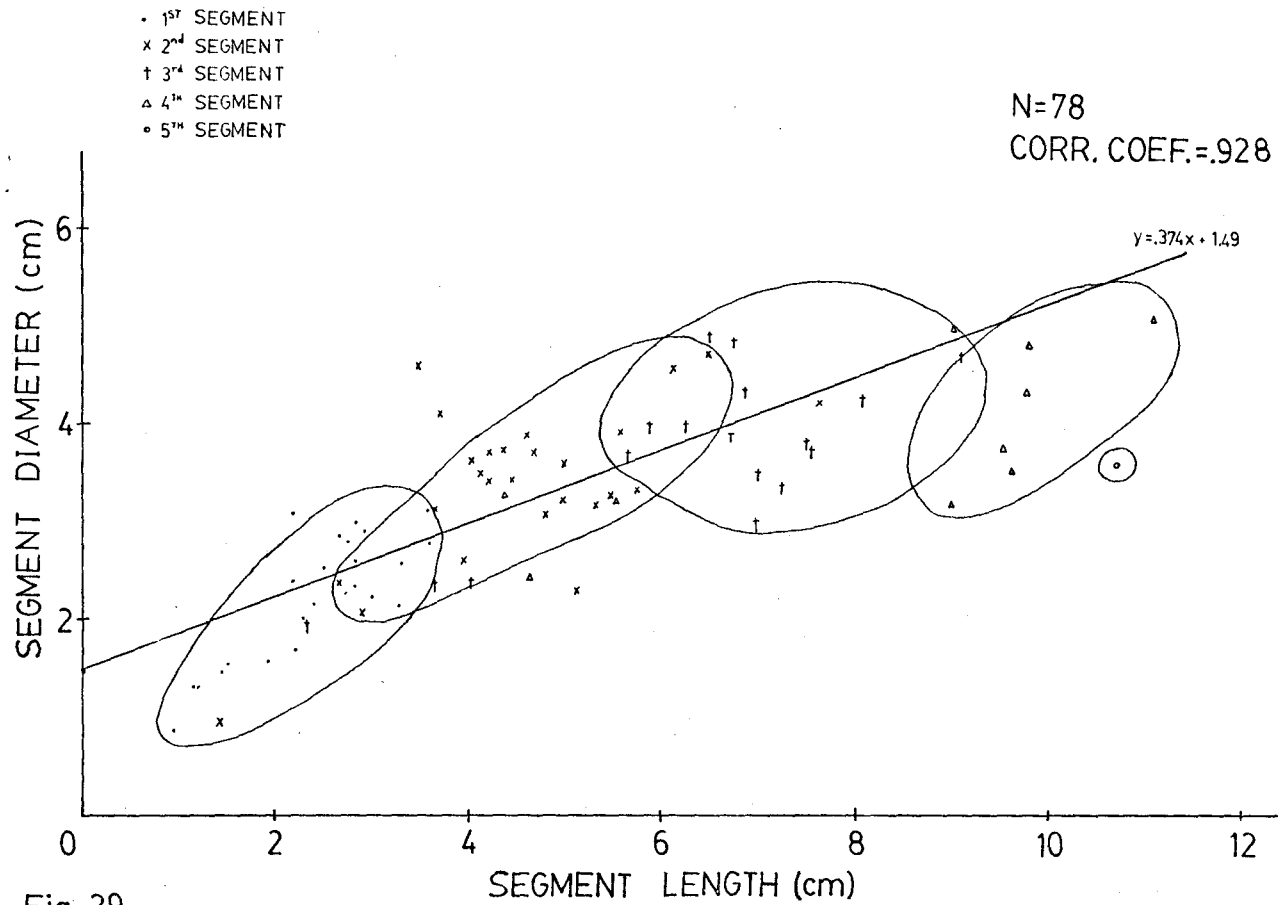


Fig. 29

Fig. 29: Segment Length vs. Segment Diameter.

LINEAR REGRESSIONS

SEGMENT 1	N=25	$y = .74x + .45$	CORR. COEF. = .83
SEGMENT 2	N=25	$y = .44x + 1.46$	CORR. COEF. = .69
SEGMENT 3	N=17	$y = .39x + 1.22$	CORR. COEF. = .76
SEGMENT 4	N=11	$y = .25x + 1.78$	CORR. COEF. = .25

- 1st SEGMENT
- x 2nd SEGMENT
- † 3rd SEGMENT
- △ 4th SEGMENT
- 5th SEGMENT

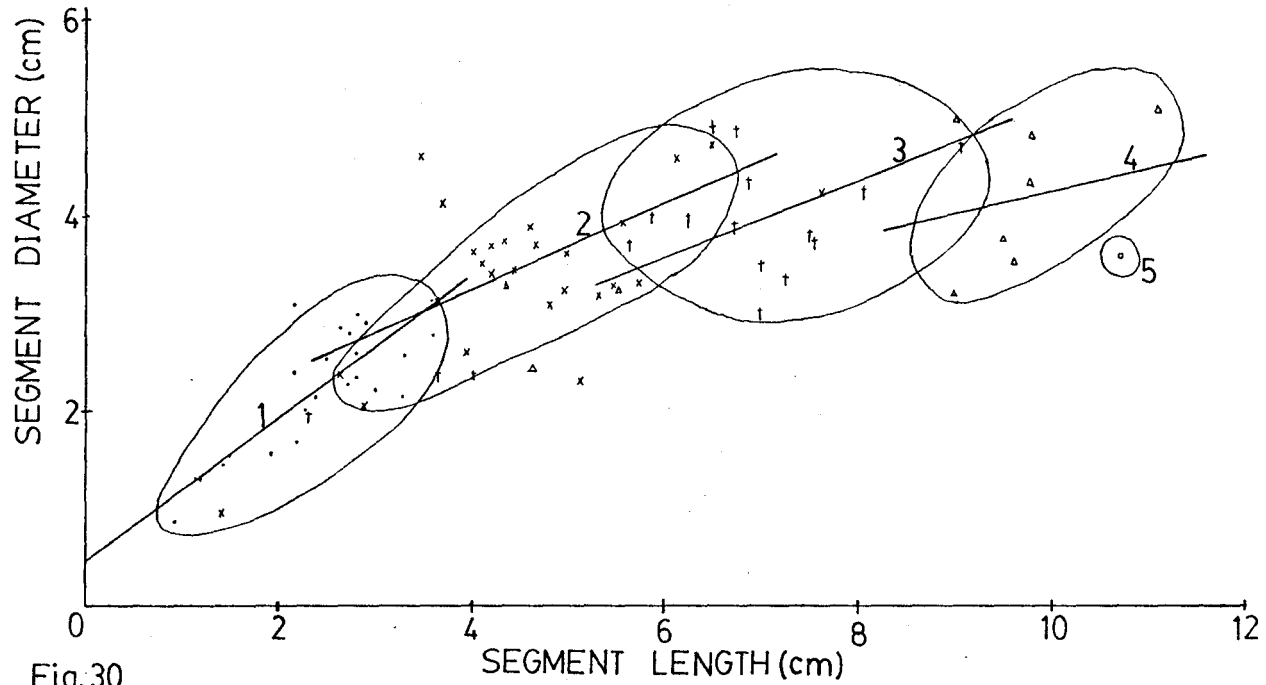


Fig.30

Fig. 30: Segment Length vs. Segment Diameter.

Table 3: SEGMENT DIAMETER INCREASE
(diameter increase from previous segment)

<u>Apex-Seg. 1</u>	<u>Segment 1-2</u>	<u>Segment 2-3</u>	<u>Segment 3-4</u>
2.15	1.76	.36	.81
3.08	1.52	.31	-.10
4.19	1.03	.90	-.60
1.80	.95	.53	.06
1.57	.69	.51	.88
2.80	.47	0.00	1.35
3.00	1.28	.32	.10
3.55	.92	.10	-.03
2.80	.76	.87	.74
2.17	2.04	1.05	.20
1.45	1.60	.04	
1.30	.05	.77	
2.56	.79	.90	
1.53	2.83	-.14	
.85	.70	.40	
2.85	1.30	-.14	
1.30	.85	-.34	
2.90	1.08		
2.13	1.56		
2.35	.97		
2.22	1.9		
3.14	2.02		
2.53	.95		
2.00	1.10		
1.68	1.10		
2.28			
3.10			
2.60			
N = 28	N = 25	N = 17	N = 10
$\bar{X} = 2.36$	$\bar{X} = 1.21$	$\bar{X} = .38$	$\bar{X} = .34$
$S_x = .75$	$S_x = .59$	$S_x = .42$	$S_x = .58$

Chapter 4 - Geniculation

4.1 Results

Many specimens exhibit a change in direction of the growth axis (symmetry axis) during ontogeny. This phenomenon is known as geniculation and reflects a sudden change in the orientation of the coral from its upright growth position. The coral then grows preferentially on the underside to return the polyp to an upright position. This is accomplished by the preferential deposition of calcium carbonate on one side of the corallite (Plates 12-16). The upright position is obviously desired by the coral and may be related to the possible presence of symbiotic photosynthetic zooxanthellae in the soft tissues. Such an upright position would allow for maximum sunlight for these zooxanthellae. The upright position and vertical growth would also allow the polyp to extend above the sediment and have greater exposure for feeding.

The growth increments are difficult to trace at the point of geniculation because they are wider on the outside curvature of the epitheca and are very fine or amalgamated on the inside curvature. This becomes more extensively developed as the angle of geniculation increases and at high angles of geniculation (60-90°) the growth increments may

Plate 13: A corallite exhibiting monthly bands and geniculation. The change of corallite shape during ontogeny as the result of a decreasing apical angle is evident.
Heliophyllum halli

Plate 14: A corallite that suffered numerous geniculation events and rejuvenescence (R).

Scale in cm.

Heliophyllum halli



Plate 15: Well preserved corallite exhibiting
geniculation (G).

Scale in cm.

Heliophyllum halli

Plate 16: Conical corallite exhibiting geniculation.

Scale in cm.

Heliophyllum halli



not be discernible on the inside curvature.

The possibility of a catastrophic event such as a storm that would upset many corals within the population was investigated. The presence of numerous disturbance lines and constrictions and the lack of complete apices presented problems for actual age counts of the geniculation. Assuming that the corals had a relatively constant growth rate then the occurrence of an event causing geniculation would have been recorded on the epithecae at similar distances from the apices. Figure 31 shows the frequency distribution of the length from the apex to the geniculation. These lengths are distributed over a relatively large range and most geniculations occur in the length range 2.0 cm to 3.9 cm even though the mean is 4.39 cm. The results for a similar investigation for corallite diameter are shown in figure 32. The mean is 3.26 cm and the data are more widely and normally distributed.

The angle of geniculation was measured for a number of specimens. This was done by estimating the growth axes of the corallite before and after geniculation (fig. 4). The geniculation occurs over a wide range of angles (fig. 33). In general, the geniculation angles are acute with a mean of 54.8° .

4.2 Discussion

A catastrophic event that disturbed numerous corals

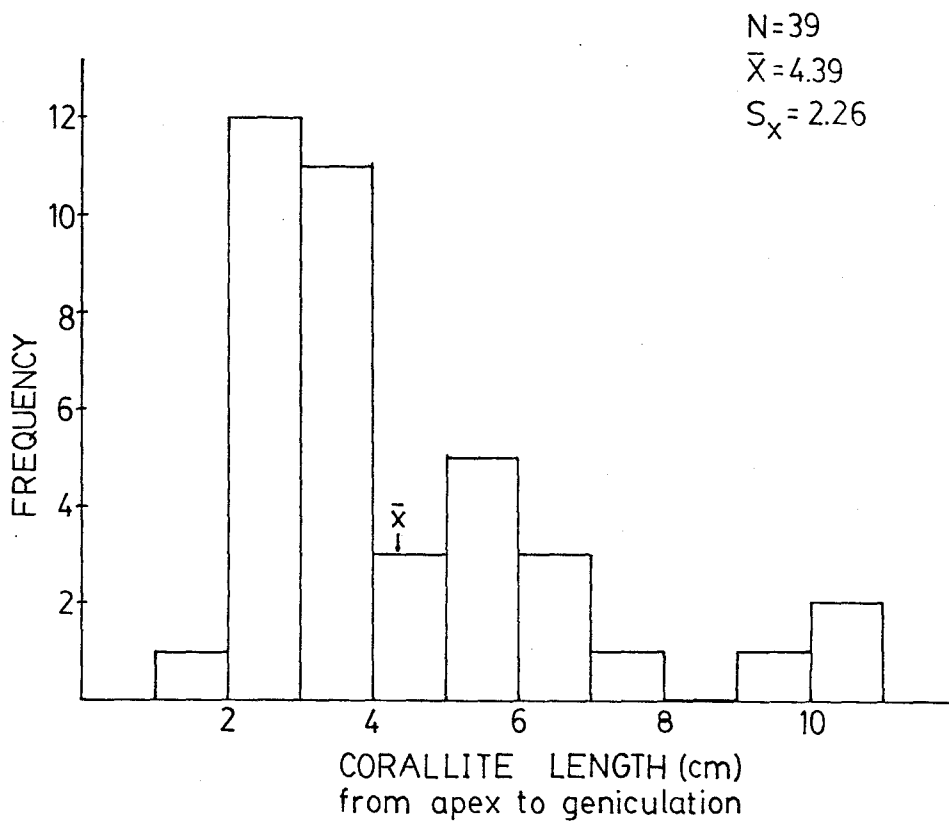


Fig. 31

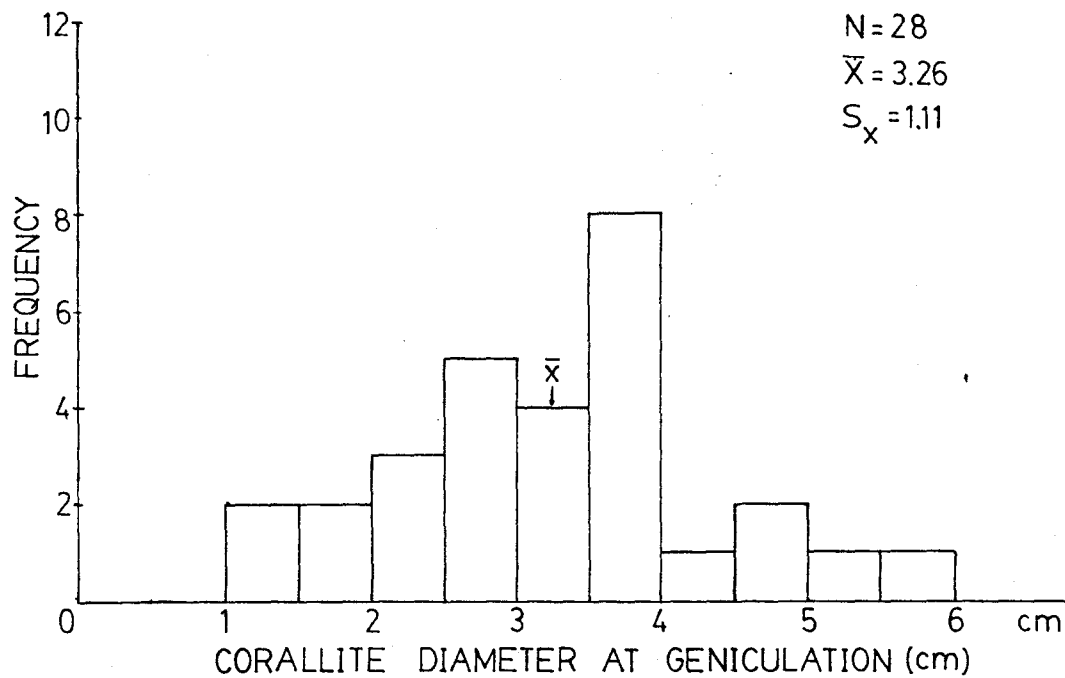


Fig. 32

within the population probably occurred. This is supported by the abundant occurrence of geniculation between 2.0 cm and 4.0 cm corallite length (fig. 31). The size range may be a reflection of growth rate variations among individuals of the coral population. Another possibility is the close occurrence of two or more such environmental events. This causative event was probably a large storm that created turbulence in the shallow water environment of the rugose corals. Other less severe storms may have been responsible for the other occurrences of geniculation thus creating the large range of corallite lengths. The corals may have become unstable as they grew and merely toppled over. This may also account for the size distribution but there seems to be strong evidence for a correlative geniculation event.

The corallite diameter data for geniculation are much less indicative of a common environmental disturbance. The mode of 3.5-3.99 cm is a very common corallite diameter range as shown in figure 32. It has been illustrated above that the corallite diameter increases rapidly in the juvenile and remains relatively constant at maturity. There is also a large variation in corallite diameter among corals of similar age. These factors account for the distribution in figure 32.

The geniculation (fig. 33) is marked by an absence of angles greater than 89° and the majority between 50° and 70° . This indicates that the corals were rarely knocked

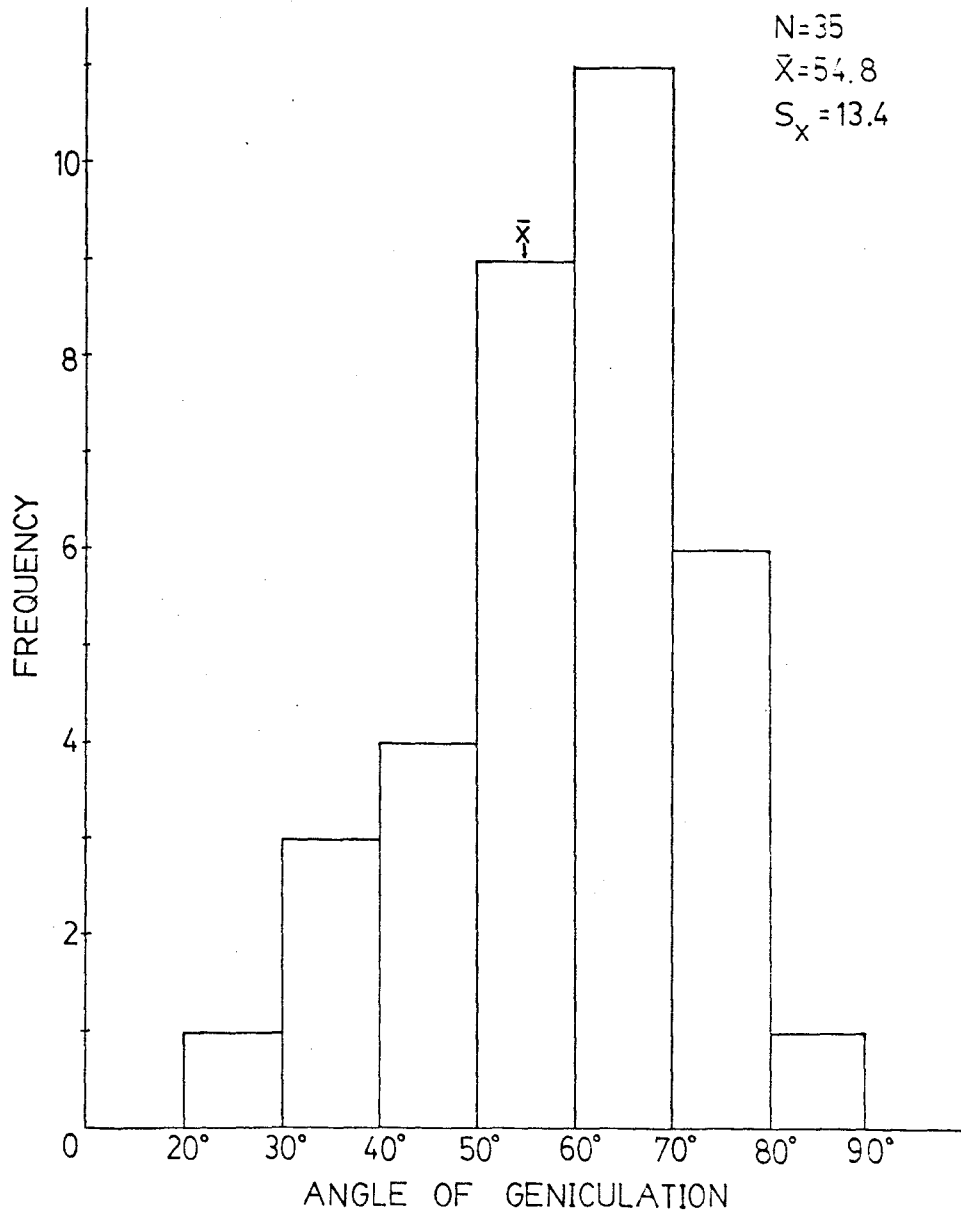


Fig. 33

over completely onto their sides. It is known that the rugose corals lived with their corallite partially buried in the soft sediment to increase stability. As a result of this stability, water disturbances would have caused the corals to be only partially knocked over and thus remained in an inclined position.

Chapter 5 - Rejuvenescence (Clarkson, 1979)

5.1 Results

Many of the sampled corals have constrictions that encircle the corallite and appear to be irregular in occurrence (Plates 12, 14). The constrictions are variable in magnitude and distance from the apex. Some corals have several constrictions while others have none. The magnitude varies from slight grooves to wider and deeper etched grooves and ledges. The constrictions are characterized by a reduction in corallite diameter which occur most often as abrupt reductions that expose the lip of an older calice. The diameter usually increased almost immediately after the constriction and the coral continued to grow and expand normally in diameter until the next period of rejuvenescence.

According the Clarkson (1979), these intervals of constriction of the coral epithecae may represent a short period of nutrient deficiency and, in order to survive, the polyp resorbed some of its own tissues. Then as nutrient supply became sufficient, the coral resumed its normal growth. This is only one possible explanation for rejuvenescence. If the occurrence of rejuvenescence is linked to environmental conditions then these features may

be correlative among specimens. The possibility of such a correlation was investigated but rejuvenescence seems to occur randomly. Some corals display several periods of rejuvenescence while others have no such occurrences. The distance from the apex also appeared to be random. The rejuvenescence occurrences are illustrated graphically in the growth histories of several specimens in figures 8-25.

Measurements of corallite diameter were collected before the constriction and at the point of constriction for numerous specimens. Differences in the two diameters were collected and a mean of .2 cm was obtained (fig. 34).

5.2 Discussion

The absence of a correlation of rejuvenescence with corallite dimensions and time may be a reflection of insufficient sample size. The wide range of diameter differences may be due to the intensity of the adverse environmental conditions and the actual degree of response by the individual to such conditions. These factors may also account for the lack of correlation. Additional factors may have been the location of individual corals with respect to water depth and habitat.

Rejuvenescence is occasionally associated with geniculation in the samples (Plate 12) but there is not a strong association between the two events. In most cases, the two events occur independently.

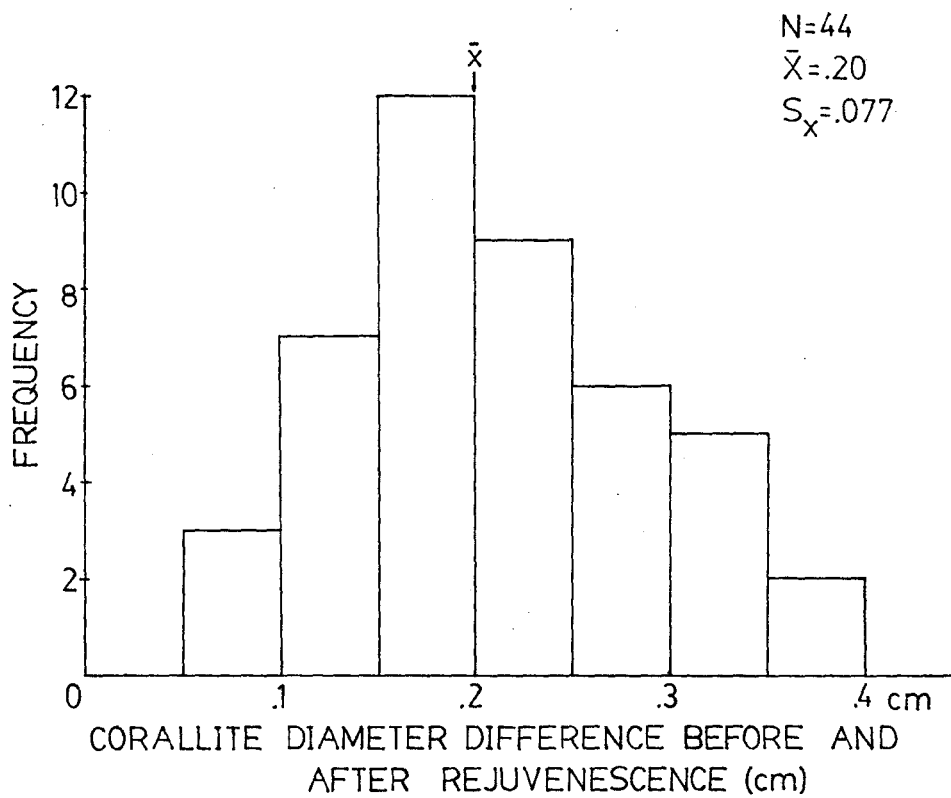


Fig.34

Chapter 6 - Bryozoans

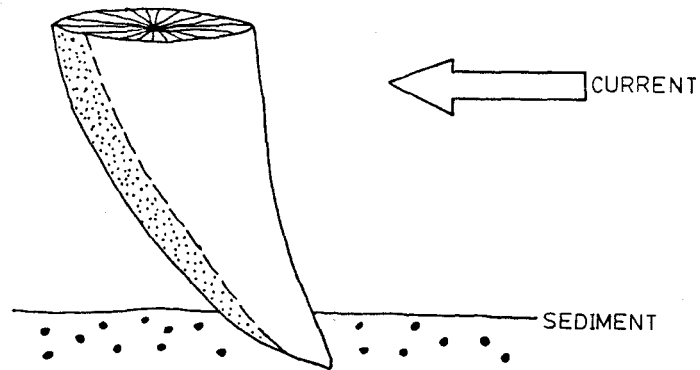
The majority of corallite epizoans are encrusting bryozoans (Table 1). Plates (17-23) show the two major types of bryozoan found on the corallites. Some of the bryozoans grew on the corallite after its death as evidenced by the occurrences of bryozoans growing over the calice (Plates 18-20). Some of these may have been emplaced while the coral was living and then grew onto the calice after the coral died.

Bryozoan zoaria are found on all portions of the corallites but they seem to be concentrated along the slightly convexly curved side of the corallite (fig. 35). On geniculate corals, the bryozoan zoaria appear to be concentrated along the underside or outer curvature of the geniculation (fig. 35b). They are also concentrated at the geniculation on the upper side of the corallite. Experiments performed by Ryland (1959) with bryozoan larvae demonstrated that the larvae actively settle in concavities in which they receive protection from abrasion. Ryland (1960) also found that the larvae are photonegative and settle on the undersurfaces of horizontal and oblique surfaces. This accounts for the distribution of bryozoans on geniculate corals. The bryozoans obviously existed on the living corals because they settled in favourable

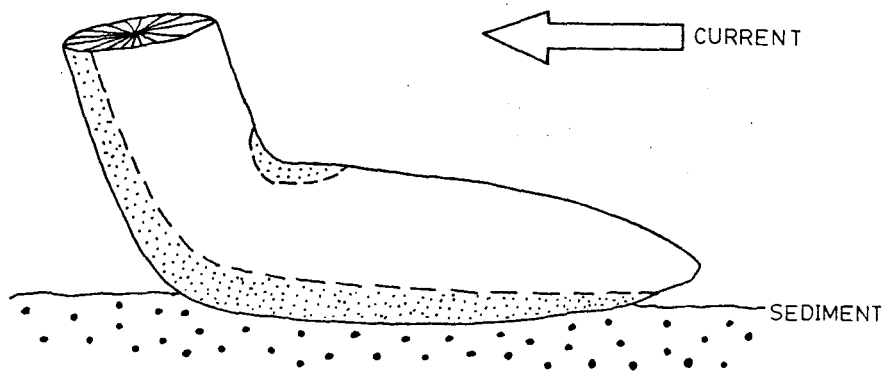
positions on the corallites after geniculation. Ryland (1960) also demonstrated that the larvae do not actively settle on upward-facing surfaces. These surfaces are unfavourable due to the settling of sediment, abrasion and exposure to light and currents.

FIG. 35

A. BRYOZOAN DISTRIBUTION ON CORALLITES



B. BRYOZOAN DISTRIBUTION ON GENICULATE CORALLITES




 REGION OF BRYOZOAN CONCENTRATION

Fig. 35: Bryozoan Distribution on Corallites.

Plate 17: Monthly banded epitheca with a large
encrusting bryozoan zoarium.
Heliophyllum halli

Plate 18: Corallite with large encrusting bryozoan that
extends over onto the calice.
Heliophyllum halli

Scale in cm.



Plate 19:

Plates 19, 20: Small corallite with common type of encrusting bryozoan that has grown onto the calice.

Heliophyllum halli

Scales in cm.

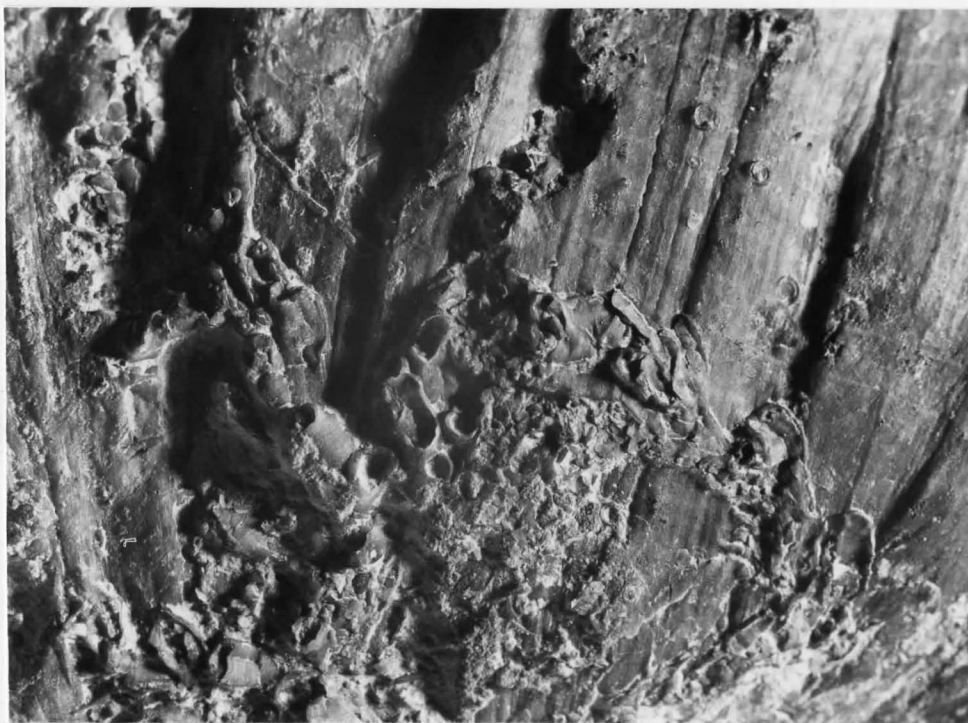
Plate 20:



Plate 21: Scale in cm.

Plates 21, 22: Corallite epithecae with a common type
of encrusting bryozoan.
Heliophyllum halli

Plate 22: Magnification (X 16)



Chapter 7 - Diagenesis

The removal of the coral epithecae of some specimens (Plate 6) may have occurred prior to deposition. The epithecae may have been partially dissolved by percolating groundwaters since deposition.

Small diagenetic aggregates of hematite rosettes occur on some of the coral epithecae (Plates 8, 21, 24). The aggregates are visible with the unaided eye but the tiny, vertically arranged hematite blades that form the rosettes can be observed only with magnification. The source of iron is probably the clay minerals of the shale unit within the Hungry Hollow Formation and other shales above and below this formation in the stratigraphic column. The iron is liberated during chemical weathering of the clay minerals and then transported in solution by groundwater to be precipitated on the coral epithecae.

Plate 23: Corallite with Cycle II (monthly) bands,
encrusting bryozoans and hematite on the
epitheca.
Heliophyllum halli

Plate 24: Monthly banded epitheca with numerous
aggregates of hematite rosettes (h).
Heliophyllum halli



Chapter 8 - Conclusions

During the Middle Devonian, the portion of North America near Arkona, Ontario was a shallow marine shelf environment covered by a warm epicontinental sea that deepened to the west into the Michigan Basin. This shelf would have been characterized by a stable marine salinity, turbulent to periodically calm water conditions along with moderate light intensity, temperature and oxygen supply. These conditions were ideal for inhabitation by crinoids, bryozoans, trilobites, brachiopods and colonial and solitary corals.

The environmental conditions of this shallow shelf sea were probably relatively stable. The secreting tissues of the rugose corals deposited thin accretionary accumulations of calcium carbonate daily except when adverse conditions may have caused the coral to omit such deposition for one or two days. This daily cyclicity probably represents solar days. Evidence by Barnes (1972) suggests that corals with photosynthetic symbiotic algae in their tissues have their calcification enhanced by the photosynthetic activity of these algae.

Once every 30.38 days a groove or reduction in corallite diameter occurred. These grooves define a monthly band. This monthly periodicity may be referred to as a synodic month (Clark, 1974) which is defined as the period

between consecutive new moons. The monthly cyclicality may have been caused by a lunar breeding periodicity triggered by the illumination of a full moon (Scrutton, 1965). A mean monthly corallite growth rate (vertical) of .377 cm was observed. The growth of the corallites is anisometric and exhibits no relationship between monthly growth rate and diameter increase.

Thirteen monthly cycles comprise a yearly growth cycle according to Wells (1963) and Scrutton (1965). Clark (1974) notes that this annual rhythm is well developed in areas of strong seasonal variation but absent or poorly developed in areas where seasonal variation is slight. The approximate 33°S paleolatitude of the study area probably experienced slight seasonal variations thus accounting for the poorly developed annual cyclicality observed.

Westerly storms would have interrupted the stable shelf community periodically. Such storms may have been responsible for major changes in wave activity, turbidity, light intensity, temperature, substrate stability and salinity. Any one of these environmental disturbances could have produced a disturbance line on the coral epithecae. The disturbance lines would be correlative among the individuals of the coral population affected by the disturbance. Changes in wave action or substrate stability caused by these storms were probably responsible for the geniculation observed in many of the coral specimens. The

occurrence of a storm sufficiently large to topple numerous members of the population and subsequent geniculation occurred when the corals were 2.0-4.0 cm in height. An adverse environmental condition such as nutrient deficiency was probably responsible for rejuvenescence in random members of the coral population. Bryozoan larvae actively settled on selected portions of the corallites such that the larvae were sheltered from abrasion, water currents and light.

The correlative, frequent occurrence of a reduction in the monthly growth rate at approximately seven monthly bands from the apex can probably be attributed to adverse conditions that affected the coral population. A similar but less obvious correlation occurs at fourteen monthly bands from the apex. The large variability of growth lines and occurrences of disturbance lines supports the idea of a shallow-water environment. Deep-water environments would be much less susceptible to atmospheric and hydrospheric disturbances because they would lie below normal fair-weather wave base of 10-15 m. Such environments would be affected only by storm waves with a base of 15-40 m (Dr. M.J. Risk, personal communication).

The shallow shelf areas were carbonate platforms upon which lime mud was deposited. The rugose coral assemblage lived in somewhat deeper waters further offshore. The occurrence of an unusually large storm (hurricane)

heading in an easterly direction destroyed this shelf community of the rugose corals by intense wave action. The organisms were transported inland and deposited unconformably on the lime mud. Shortly after the storm had subsided, the conditions returned to normal and the lime mud continued to be deposited unconformably on the skeletal debris deposited by the storm. This may be indicated by the lack of trace fossils or bioturbation within the shale unit. This is only a possible mechanism but it does account for the highly fossiliferous shale unit bounded stratigraphically above and below by much less fossiliferous limestone units as observed in the Hungry Hollow Formation. The rapid deposition mechanism accounts for the sharp contacts between the shale and limestone units and the lack of sorting of fossil fragments within the shale. It also accounts for the presence of the clay particles that comprise the shale. A persistent current or reworking of this debris would have winnowed the clay from the debris. The debris would have been sorted, rounded and abraded as the result of such erosional activity. The movement of the storm in an easterly direction is consistent with an approximate east-west orientation of the long axes of the conical corallites in the shale beds and the movement of present-day storms.

A storm depositional mechanism appears to have been responsible for creating the fossiliferous shale of the Hungry Hollow Formation. The single corallites from

different areas of the population could have been intermixed and deposited together by such an mechanism. This may have accounted for the poorly defined correlations and may have obliterated subtle correlations that affected only portions of the whole population. Thus only the major disturbances common to the majority of the individuals of the population would remain correlative and this is a major factor in the analysis of such correlations.

APPENDICES

Appendix A: Number of Growth Cycle I Lines per
Cycle II Band.

<u>No. of Cycle I</u>	<u>No. of Cycle I</u>	<u>No. of Cycle I</u>	<u>No. of Cycle I</u>
28	31	29	28
29	30	30	30
33	29	32	31
32	31	28	29
31	30	29	28
29	33	31	29
30	29	33	30
30	28	32	31
31	30	31	32
32	31	30	33
28	32	29	34
29	34	30	29
31	30		

$$N = 50$$

$$\text{Mean } (\bar{X}) = 30.38$$

$$S_x = 1.63$$

Appendix B: Corallite length of Geniculation From the Apex

<u>Sample #</u>	<u>Length (cm)</u>	<u>Sample #</u>	<u>Length (cm)</u>
11d	10.8	11L	5.49
9j	3.30	6a	6.61
	9.95	14d	5.50
Q3	5.60	1k	2.60
3o	5.80	7e	3.30
7p	7.10	13g	2.50
7r	10.50	12d	3.40
7h	4.80	5e	2.50
9d	3.50	11dd	3.50
8h	3.50	14b	4.51
	5.90	15a	2.50
Q16	6.50	Q10	2.52
11h	2.50	Q19	2.73
10b	3.00	Q20	2.42
	6.60	Q25	2.51
11r	4.50	Q24	3.44
1g	2.20	15d	3.51
11w	2.30	9z	3.72
Q11	3.51	4k	3.09
1bi	2.62		

$$N = 39$$

$$\bar{X} = 4.39$$

$$S_x = 2.26$$

Appendix C: Corallite Diameter Difference (dD) Before and After Rejuvenescence

<u>dD (cm)</u>	<u>dD (cm)</u>	<u>dD (cm)</u>	<u>dD (cm)</u>
.20	.25	.17	.13
.15	.21	.24	.17
.31	.14	.18	.21
.20	.09	.11	.19
.13	.19	.21	.16
.10	.24	.25	.07
.12	.27	.24	.08
.30	.31	.31	.27
.15	.27	.27	.37
.16	.35	.32	.22
.15	.15	.12	.13

$$\begin{aligned}
 N &= 44 \\
 \bar{X} &= .20 \\
 S_x &= .077
 \end{aligned}$$

Appendix D: Corallite Diameter (D) at Genuculation and Genuculation Angle (G)

<u>Sample #</u>	<u>D (cm)</u>	<u>G°</u>
14d		87
7b	1.64	65
3o	5.83	75
13g	2.63	55
12d	2.36	55
7c	3.49	58
13h	3.59	62
15y	3.76	68
9j	4.75	65, 35
16a	3.96	55
1k	1.14	54
Q5	2.92	78
7r	5.09	73
Q16	3.21	70
11f	3.99	63
11L		55
9d	2.59	49
8h	3.75	50
9b		60
11w		62
11d	3.88	45
7p	3.88	65
11h	2.10	35
7a	1.42	51
11Lr	3.12	70
5g	3.51	60
10b		76
11n	2.53	50
11Lcc	3.35	47
11a	4.92	61
11bi	2.41	37
1g	1.70	60
Q3	4.2	42, 25
N =	28	35
\bar{X} =	3.26	54.8
S _x =	1.11	13.4

Appendix E: Segment Measurements of Corallite Width (W)(cm)
and Diameter (D)(cm)

Sample #	Seg. 1		Seg. 2		Seg. 3		Seg. 4		Seg. 5	
	W	D	W	D	W	D	W	D	W	D
7r	3.28	2.15	2.27	3.91	2.52	4.27	3.05	5.08		
9j	2.16	3.08	1.30	4.60	3.03	4.91	3.31	4.81		
3o	6.50	6.00								
7t	4.36	4.19								
1g	2.15	1.8								
3d	1.92	1.57	2.01	2.60	2.76	3.5				
1f	2.74	2.80	1.60	3.75						
3zz	2.80	3.00	1.40	3.69						
8a	3.24	3.55								
7p	3.60	2.80	1.90	3.27	2.0	3.8	1.5	3.2	1.7	3.59
3q	2.30	2.15	2.17	3.45	1.77	3.96				
7o	1.42	1.45	1.23	2.37	1.00	2.37	0.95	2.43	2.15	2.50
6a	1.16	1.30	1.73	2.06	1.13	2.38	1.50	3.26		
13z	3.30	2.56	2.84	4.60	2.93	4.70				
7s	1.50	1.53	2.13	3.13	2.26	4.00				
12a	0.91	0.85	0.50	0.90	0.90	1.95	2.04	3.30	2.0	
14a	2.67	2.85	1.34	3.64	1.64	3.68				
15a	1.15	1.30	2.55	4.13	3.03	4.90	2.30	5.00		
15c	2.90	2.90	2.10	3.60						
Q1	2.40	2.13	1.80	3.43	2.64	4.33	2.93	4.30		
15d	2.80	2.35	2.52	3.20	1.66	3.06	2.54	3.80		
15b	3.00	2.22	2.75	3.30						
Q2	3.60	3.14	2.86	4.70						
Q3	2.50	2.53	1.60	3.50	2.60	3.90				
Q4	2.30	2.00	2.66	3.90	2.80	3.76				
Q6	2.20	1.68	2.45	3.70	2.60	3.36	2.36	3.56		
13q	2.73	2.28	2.16	3.23						
13r	4.70	3.10	2.80	4.20						
Q7	4.70	2.60	2.33	3.70						

Appendix F: Cycle II Band Measurements (cm)

w = width; d = diameter

	Sample									
	1a _{ii}		3d		3e		3o		6a	
	w	d	w	d	w	d	w	d	w	d
1										
2										
3	.1	.62	?	?	?	?	?	?	?	?
4	.23	.80	.7	1.6	.56	1.79	.3	1.56	.5	2.03
5	.47	1.20	.75	1.74	.57	2.7	.64	2.06	.52	2.1
6	.48	1.66	.4	2.04	.80	3.5	.62	2.84	.60	2.4
7	.20	1.86	.7	2.59	.40	3.9	.45	3.22	.40	2.66
8	.30	2.2	.9	2.9	.42	3.9	.65	3.69	.40	2.83
9	.52	2.63	.8	3.23			.53	4.26	.42	2.86
10	.58		.87	3.56			.70	4.73	.43	3.21
11				3.58			.61	5.25	.39	3.53
12							.80	5.45	3.8	3.66
13							.61	6.0	.40	3.95
14									.48	
	7d		7k		7o		7p		7r	
	w	d	w	d	w	d	w	d	w	d
1					.3	.15				
2					.2	.31				
3					.3	.47			?	?
4			?	?	.28	.77			.31	2.47
5	?	?	.5	1.59	.31	.99			.4	2.45
6	.32	1.36	.41	1.91	.32	1.46			.5	2.87
7	.46	1.7	.40	2.27	.40	1.73	?	?	.66	3.67
8	.56	2.22	.45	2.8	.39	2.1	.29	1.68	.4	3.78
9	.51	2.43	.40	2.61	.4	2.39	.36	1.76	.5	3.93
10	.46	2.62	.50	2.63	.36	2.21	.38	2.13	.62	3.63
11	.29	2.64	.45	3.14	.46	2.36	.39	2.43	.4	3.73
12	.40	2.71	.49	3.51	.75	2.41	.39	2.5	.41	3.75
13	.31	2.74	.41	4.09	.32	2.57	.4	2.7	.39	4.04
14					.39	2.92	.45	2.87	.37	4.21
15					.45	3.3	.30	2.91	.26	4.25
16					.41	3.36	.38	3.22	.22	4.23
17					.38	3.46	.42	3.26	.35	4.16
18							.32	3.58	.28	4.27
19							.3	3.6	.32	4.33
20							.29	3.62	.55	4.63
21							.3	3.77	.25	4.69
22							.3	3.8	.21	4.7
23									.30	4.65
24									.25	4.66
25									.32	4.9

* Cycle II from apex

		Sample									
		7d		7k		7o		7p		7r	
		w	d	w	d	w	d	w	d	w	d
26										.31	4.92
27										.26	5.06
28										.31	4.98
		8a		9a		9g		9j		11d	
		w	d	w	d	w	d	w	d	w	d
1		?	?	.3	.42	?	?				
2		.31	1.14	.36	.73	.3	.47				
3		.5	1.70	.38	1.66	.27	.63				
4		.5	2.15	.4	2.09	.26	.79				
5		.59	2.84	.37	2.25	.31	1.16				
6		.35	3.2	.4	2.75	.38	1.56			?	?
7		.25	3.33	.38	2.99	.21	2.04			.5	3.18
8		.27	3.52	.37	3.43	.35	2.4			.31	3.32
9						.22	2.62	?	?	.31	3.54
10								.3	4.52	.29	3.61
11								.48	4.46	.3	3.63
12								.22	4.4	.23	3.77
13								.25	4.36	.35	3.76
14								.22	4.4	.37	3.81
15								.20	4.47	.30	3.9
16								.21	4.41	.26	4.06
17								.22	4.45	.28	4.09
18								.3	4.6	.36	4.02
19								.19	4.62		
20								.31	4.78		
21								.3	4.92		
22								.32	4.88		
23								.3	4.85		
24								.3	4.84		
25								.15	4.85		
26								.28	4.84		
27								.22	4.72		
28								.25	4.75		
29								.3	4.73		
30								.22	4.66		
31								.2	4.69		
32								.28	4.64		
33								.3	4.73		
34								.3	4.76		
35								.2	4.75		

* Cycle II from apex

	Sample									
	11f		11j		11p		11s		11x	
	w	d	w	d	w	d	w	d	w	d
1										
2									?	?
3			?	?	?	?			.09	.36
4			.37	1.32	.2	1.12	?	?	.1	.42
5			.35	1.81	.26	1.31	.25	1.15	.11	.55
6	?	?	.4	2.3	.5	1.98	.26	1.50	.14	.62
7	.5	3.13	.41	2.75	.52	2.58	.29	1.67	.16	.75
8	.63	3.32	.41	2.98	.5	3.07	.46	2.18	.18	.94
9	.57	3.47	.39	3.4	.47	3.7	.48	2.56	.2	1.06
10	.48	3.64	.31	3.62	.38	3.91	.45	2.99	.22	1.3
11	.49	4.08	.35	3.95	.52	4.22	.39	3.26	.25	1.47
12	.48	3.9			.5	4.39	.35	3.50	.27	1.49
13	.36	3.96			.51	4.65	.32	3.87	.31	1.59
14	.37	3.96					.28	3.88	.27	1.74
15	.38	3.97					.30	4.04	.35	2.1
16							.35	4.2	.32	2.0
17							.29		.35	2.15
18							.30		.38	2.38
19									.36	2.5
20									.30	2.6
21									.23	2.48
22									.2	2.45
23									.22	2.5
24									.28	2.52
25									.45	2.8
26									.23	2.82
27									.26	2.8
28									.21	2.97
29									.24	2.9
30									.3	2.93

* Cycle II from apex

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