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PERIODIC DEVELOPMENT OF DIMETRISM IN SOME FAVOSITID CORALS

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Sporadic dimetrisism in some specimens of two English Wenlock favositid coral species, *Favosites multipora* and *Paleofavosites rugosus*, is investigated by serial sectioning. The dimetric appearance is found to be periodically developed within a colony where it occurs and to be caused by fluctuating rates of corallite increase. Peak increase corresponds in a regular pattern to other periodic features in these corals. Zones of close-spaced tabulae, thickened corallite walls and well developed septal spines form bands of denser growth occurring with an annual periodicity and it is concluded that increase and therefore dimetrisism is also seasonally controlled in these corals. Entraining factors and the cause of modifications in the relative timing of peak increase are discussed. Dimetrisism in these corals is considered to be wholly of ecophenotypic origin and of no taxonomic significance.

Key words: Tabulata, coral increase, Silurian.

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INTRODUCTION

The recognition of species in many groups of corals is complicated by a considerable measure of phenotypic variation resulting from the influences of environmental variables on growth processes. Favositid tabulate corals are particularly affected in this way (Jones 1936; Philip 1960; Sutton 1966; Powell and Scrutton 1978; Stel 1978). Ecophenotypic variation in the development of such skeletal elements as tabulae, septal spines and corallite wall thickness in favositids is well known and has suggested mean adult corallite size (measured usually as a diameter) as the most useful primary species discriminator in these corals. In addition, some favositids exhibit a bimodal distribution of corallite size (dimetrisism) and this feature has also been regarded in some cases as taxonomically significant (for example in *Favosites forbesi* Edwards et Haime 1851: 238; Stel 1978: 96). In other cases, however, dimetrisism has been related to variable growth rates (Sokolov 1955; Ross 1953: 71, although

she also quotes dimetrisism as a diagnostic character) or the maintenance of a high rate of corallite increase (Jones 1936), both implying environmental control rather than any fundamental genetic programming. True dimorphism in tabulate corals appears to be very rare. Oliver (1966, 1975) has described dimorphism in *Striatopora flexuosa*, *Lecfedites canadensis* and *Bractea arbor*, with the two latter characterised by striking dimetrisism. He claimed, however, that this dimorphism was based on more than just bimodal size distribution, which in itself is insufficient basis for significant polyp differentiation to be assumed (Oliver 1975: 1). Stel (1978: 100) has questioned whether even these examples are truly dimorphic (but see Oliver, 1979: 189). It seems clear that for simple dimetrisism to be considered of genetic significance it should be necessary to prove a sustained differentiation between members of the two corallite size classes, which is unlikely to be ecophenotypically maintained.

During a taxonomic revision of tabulate corals from the Wenlock (Middle Silurian) of the English Midlands, Welsh Borderland and South Wales undertaken by one of us (J. H. P.), sporadic dimetrisism was noticed among the favositids. In order to test its significance we undertook a programme of serial sectioning of selected colonies. So far, six colonies have been prepared and four analysed in detail. Of the latter, three are specimens of *Favosites multipora*, one a control colony showing no sign of dimetrisism, and one a specimen of *Paleofavosites rugosus*. The two remaining colonies are both examples of *P. rugosus*. All the material is housed in the British Museum (Natural History), London.

METHODS

Blocks of between 4 cm² and 12 cm² surface area were cut from each colony and individually cemented to a steel plate so that, as closely as possible, growth zones in the coral were parallel to the surface of the plate. The plate was mounted on the magnetic chuck of a small lathe fitted with a micrometer feed and a diamond impregnated cup wheel. Sections were prepared by the acetate peeling of successively ground parallel surfaces. Peels were taken at various intervals from 0.1 to 1.0 mm but all the data reported here are taken from peels 2.0 mm apart, which was found to be the most suitable spacing for this study.

In each section, the size of all corallites falling within a 1 cm² area was recorded. In successive sections within a set, the 1 cm² area was positioned so that, as far as possible, the same corallites were measured in each case. With changes in size during hystero-ontogeny, some corallites eventually pass outside the measured area and new offsets appear. Thus the number of corallites on which the histograms of figs. 5 and 6 are based varies (Table 1). Even so, a large number of corallites can be traced through a complete set of sections representing up to 2.6 cm of vertical growth (fig. 5b).

Most previous workers have used diameter or an equivalent linear parameter as a measure of size in massive corals. Scrutton (1968) introduced mean area as a measure of size but Stel (1978) was the first to measure the area of individual pris-

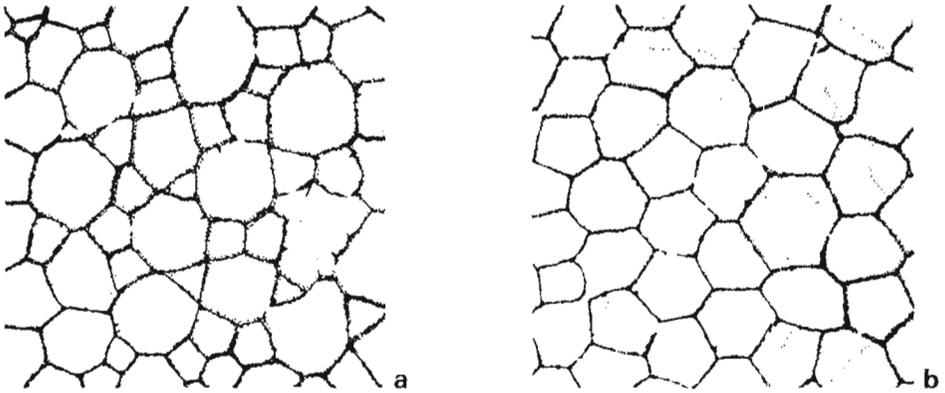


Fig. 1. *Favosites multipora* showing a dimetric, b non-dimetric sections from vertically superposed areas of the same colony. $\times 5$. R50137, sections 20 (a) and 24 (b). Silurian, Wenlock Series, Much Wenlock Limestone, reef facies; Shadwell Rock Quarry, 1 km N of Much Wenlock, Salop, England (National Grid ref. SJ 62620090).

matic corallites in section. Stel (1978: 50) made use of a sophisticated electronic planimeter which may not be readily available, but standard mechanical planimeters such as the instrument used in this study (Clarkson's compensating polar planimeter) are both commonly used in cartography and relatively cheap to buy. Measurements were made on $\times 10$ photographs and were reproducible to an accuracy of within 5%. Although various attempts have been made to standardise linear measurements (for example Sutton 1966: 257), there is little doubt that area, which can be measured easily and accurately with a planimeter, is a much better estimator of corallite size than diameter and we strongly recommend its more widespread use. It should be

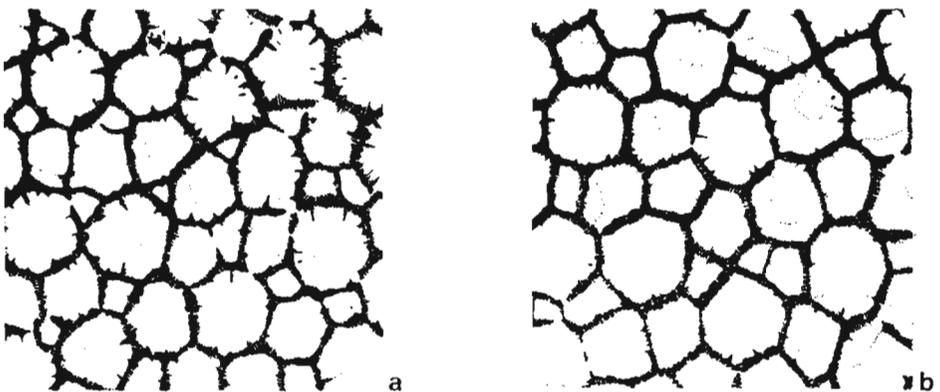


Fig. 2. *Paleofavosites rugosus* showing a strongly dimetric and b weakly dimetric sections from vertically superposed areas of the same colony. $\times 5$. R50140, sections 17 (a) and 21 (b). Silurian, Wenlock Series, Much Wenlock Limestone, inter-reef facies; Lilleshall Quarry, 4.5 km SW of Much Wenlock, Salop, England (SO 57409675).

noted, however, that frequency distributions of area and diameter measurements are not directly comparable, a normal distribution in the former appearing negatively skewed in the latter.

ANALYSIS OF DIMETRISM

Visual inspection of the sets of serial sections for the colonies showing dimetrisism indicate that this is a variable effect. Some levels are strongly dimetric whereas closely adjacent levels in the same colony, involving largely the same corallites, show little or no dimetrisism (figs. 1 and 2). Data for the four colonies analysed in detail are illustrated in figs. 5 and 6 as a series of frequency histograms with 0.5 mm² class intervals. Sections showing strong dimetrisism equate with bimodal or polymodal distributions with a strong peak of corallites 1 mm² or less in area, whereas sections with little or no visual dimetrisism correspond to unimodal distributions or weakly polymodal distribution lacking a peak of small corallites. In the histograms, new corallites, which arise by lateral increase, are distinguished by shading. The fluctuation in dimetrisism can be seen to result from the periodic incidence of increase (fig. 5a) or periodic peaks in the formation of offsets (figs. 5b, 6c and d). The new corallites then grow in size to merge with the main peak of the distribution.

The periodically dimetric effect is most marked in colonies undergoing moderate rates of expansion, with corallites subparallel to weakly diverging in longitudinal section (lower part of fig. 3a). A particularly striking contrast is between figs. 1a and 1b which correspond respectively to sections 20 and 24 in fig. 5a. Colonies undergoing more rapid expansion, with markedly diverging corallites in longitudinal section (figs. 3c, 4), tend to show a fluctuating dimetric state with all traces of bimodality rarely lost (figs. 5b, 6c, d). They also show a much greater spread of corallite sizes and a tendency to flattened, polymodal distributions. The control specimen, which shows no dimetric effect, proves to have a very low incidence of increase (figs. 6a, b). It shows little or no colonial expansion in the block sectioned, with parallel to converging corallites in longitudinal section (fig. 3b), and the histograms are strongly unimodal with a narrow range of corallite size when compared with the other examples of the same species (figs 5a, 6c, d). A similar effect is seen in the upper part of R50137 (figs. 5a, 3a) where the corallites are also converging.

Part of the spread in corallite size at the higher end of some histograms in specimens R50137, R50139 and R50140 is due to the growth of 'extra-large' corallites. They tend to become more prominent approaching periods of peak increase (fig. 5a, sections 20, 22; fig. 5b, sections 29, 31; figs. 6c, d, sections 12, 30, 44). Mostly they are established adult corallites over the vertical distance sectioned, but age is not a necessary prerequisite and young corallites can join this 'extra-large' group within 14 mm of their first appearance. New offsets are located around these 'extra-large' corallites which then usually decrease in size as the juveniles grow (fig. 7). It is this size contrast between the small number of 'extra-large' corallites and the new offsets which heightens the dimetric appearance at levels of peak increase.

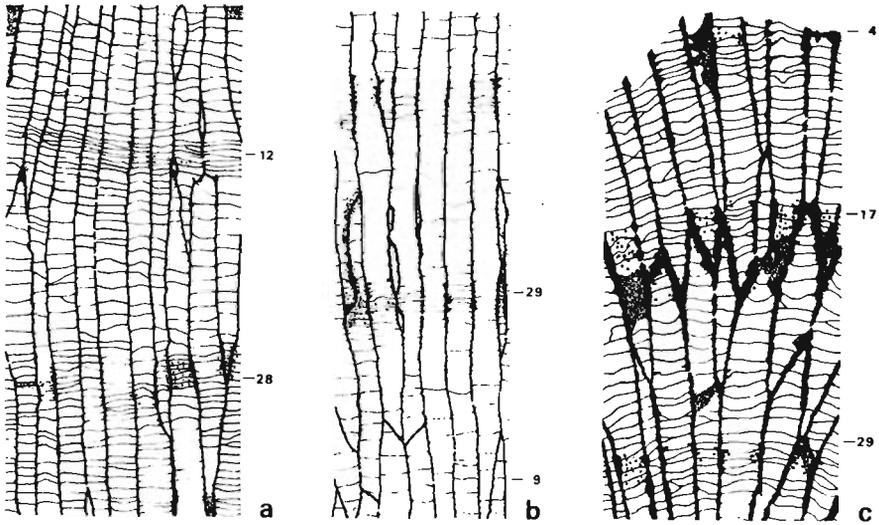


Fig. 3. Longitudinal sections with positions of serial cross-sections indicated. $\times 2.5$. a, b *Favosites multipora*. a R50137. Horizon and locality as in fig. 1. b R50138, Silurian, Wenlock Series, Much Wenlock Limestone, inter-reef facies; disused trackside quarry, nr. Checkley, Woolhope, Hereford and Worcester, England (SO 61203810). c *Paleofavosites rugosus*. R50104. Horizon and locality as in fig. 2.



Fig. 4. Longitudinal section of colony with marginal notching and sediment incorporation. Positions of serial cross-sections indicated. Natural size. *Favosites multipora*. R50139. Silurian, Wenlock Series, Much Wenlock Limestone, reef facies; locality as in fig. 3b

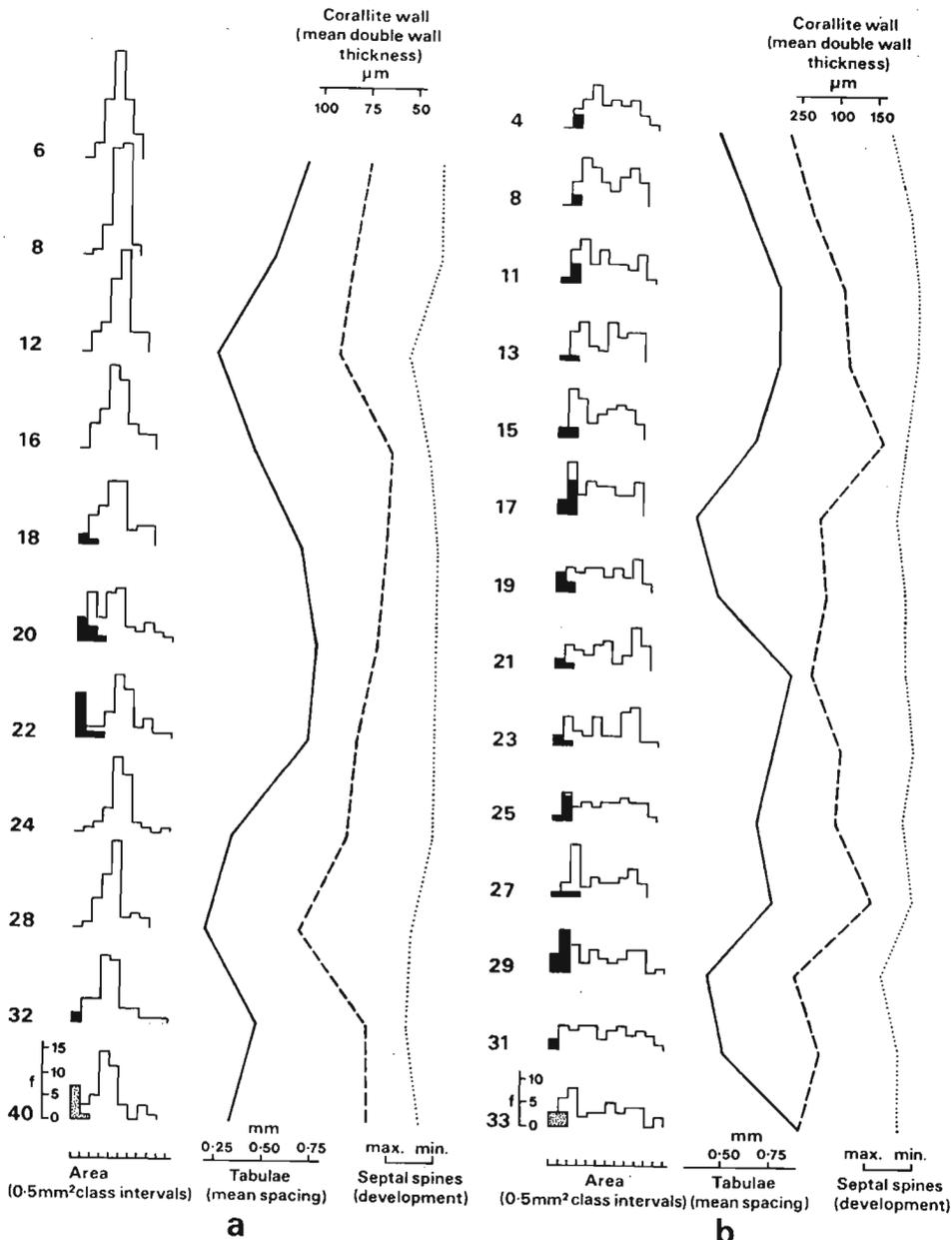


Fig. 5. Frequency histograms of corallite areas plotted in 0.5 mm² class intervals, and variations in mean tabulae spacing (solid lines), mean corallite double wall thickness (dashed lines), and development of septal spines (dotted lines) for series of serial cross-sections spaced 2 mm apart. Shaded parts of histograms represent new offsets (estimated where stippled). Direction of growth towards top of page. For further details see text. *a Favosites multipora*. R50137. Horizon and locality as in fig. 1. *b Paleofavosites rugosus*. R50140. Horizon and locality as in fig. 2.

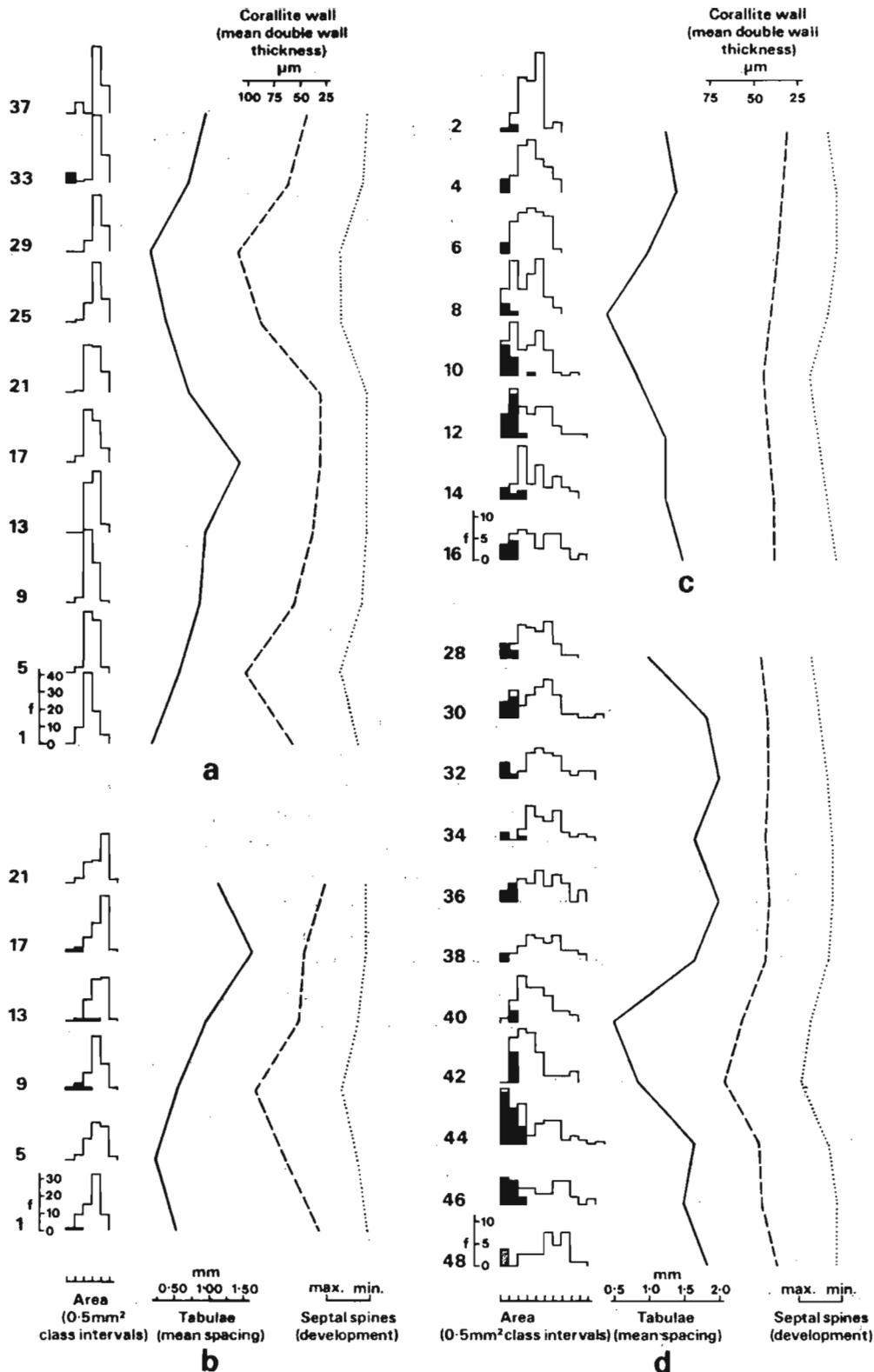


Fig. 6. Legend as for fig. 5. *Favosities multipora*, a, b R50138. Horizon and locality as in fig. 3b. c, d R50139. Horizon and locality as in fig. 4.

However, it cannot be demonstrated from the available sections whether or not the offsets arise preferentially from the 'extra-large' corallites. Otherwise they show no structural differentiation. They vary markedly in size and seem to be least successful in competition for space in the colony when this becomes more pronounced. In contrast, most juveniles show vigorous initial size increase whilst the bulk of adult corallites show rather less variation in size (fig. 8). In R50138, which shows no dimetric effect, there is no differentiation of a group of 'extra-large' corallites. They also tend to disappear in the upper levels of R50137 where no increase takes place (right-hand end of fig. 8).

RELATIONSHIP OF DIMETRISM AND INCREASE TO DENSITY BANDING

The periodicity in dimetrisism and increase in these favositids is compared with other, well established periodicities in structural elements in figs. 5 and 6. The spacing of tabulae, development of septal spines and corallite wall thickness all vary in a relatively regular pattern. Narrow zones of crowded tabulae correspond closely with thickened corallite walls and prominent septal spines to form bands of denser skeletal growth. Double wall thickness, the distance across the fused walls of two adjacent corallites, and the development of septal spines were measured in the serial cross-sections and so relate directly to the histograms. The density banding is best seen in longitudinal sections (figs. 3, 4), however, from which the sequences of mean tabulae spacings recorded in figs. 5 and 6 were obtained. The latter have been carefully related to the other data but the possibility of slight errors in correlation exists as growth surfaces in the sectioned blocks are never perfectly flat and absolutely parallel to the plane of section. The correspondence of minimum tabulae spacing with maximum wall thickness and septal development is generally good in figs. 5 and 6, and where it is slightly out of phase, this is considered to be real variation and not the result of errors in correlation.

There is a clear relationship between periods of peak increase and the density banding. In figs. 5a, b, peak increase occurs with some regularity either at the top of the dense band or closely following. One of the specimens not illustrated here, another example of *Paleofavosites rugosus* (R50141), also shows peak increase closely following zones of crowded tabulae. Even in figs 6a, b, what little increase there is follows the same pattern. It should be noted that the series in fig. 6b comes from a different area in the same set of serial sections as the lower part of fig. 6a.

The series illustrated in figs. 6c, d also shows a consistent relationship of increase to density banding but here peak increase closely precedes levels of thickened skeletal elements. This is from a small colony, much affected by sediment with pronounced contractions of surface area immediately following zones of crowded tabulae (fig. 4). In addition, a specimen of *P. rugosus* not illustrated here, although with maximum increase immediately following a dense band, shows persistently high increase with a second peak before the next zone of thickening. In this case, however, only one complete density cycle can be sectioned, close to the base of a low

discoidal colony in which initial rapid expansion may obscure any pattern. All the other specimens are from the upper parts of larger, well established colonies and contain no trace of sediment.

INTERPRETATION OF PERIODIC GROWTH FEATURES

Regular density banding is a common feature of Recent scleractinian coral skeletons and is now well established to be the result of differential growth with an annual periodicity (for example Ma 1934a, b; Knutson *et al.* 1972). Density banding is also common in Palaeozoic rugose and tabulate corals and has been regarded as an annual periodicity at least since the work of Ma (1933). The general similarity of the phenomenon in Recent and fossil corals, and the growing mass of experimental data on living corals leaves little doubt as to the validity of this deduction. In detail there is some variation in the skeletal modifications forming dense bands. In both Recent and fossil corals, thickening of skeletal elements is normally involved, although the associated closer packing of tabulae and smaller dissepiments usually prominent in rugose and tabulate corals is not always mirrored in the spacing of dissepiments in scleractinian corals (cf. Ma 1934b: figs. 7, 8, with Macintyre and Smith 1974: 279). This may relate to differences in internal structure and/or whether or not density banding is associated with marked changes in growth rate during the year. The latter is apparently not a necessary prerequisite (Weber *et al.* 1975: 140).

The favositid corals studied here show a well developed annual periodicity in growth, and the spacing of the dense bands indicates a linear growth rate of between 5 mm and 18 mm per year in this sample (5 mm—14 mm/year in *Paleofavosites rugosus* and 8 mm—18 mm/year in *Favosites multipora*). It follows that the periodicity in the formation of offsets in these corals is also annual. The pattern, however, is not completely regular and no offsets occur where they might be ex-

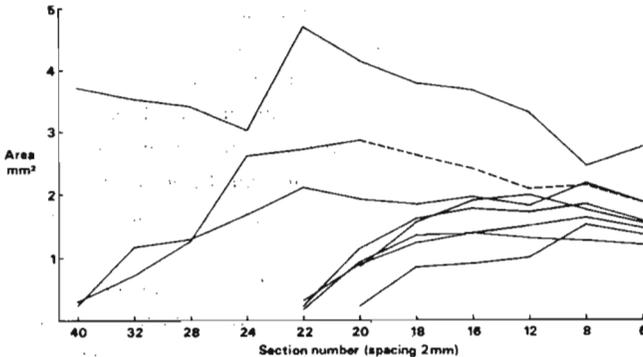


Fig. 7. Variation in corallite area of one selected 'extra-large' corallite and all offsets appearing adjacent to it through a series of serial cross-sections. Direction of growth to right. Dashed line indicates offset no longer adjacent to 'extra-large' corallite. *Favosites multipora*. R50137. Horizon and locality as in fig. 1.

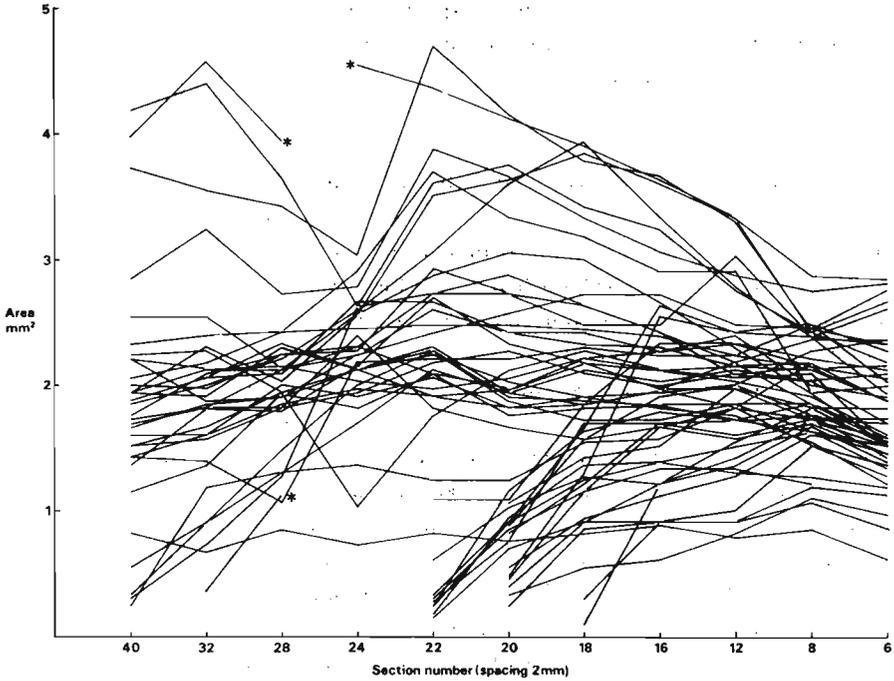


Fig. 8. Variation in corallite area of all corallites recorded throughout a series of serial cross-sections. Direction of growth to right. Asterisks indicate fusion of two corallites and continuation of resultant. *Favosites multipora*. R50137. Horizon and locality as in fig. 1.

pected in the upper part of fig. 5a and the lower part of fig. 6a. These are situations in which existing corallites are becoming smaller and corallite walls in longitudinal section are converging. We interpret this as a microenvironmental effect, with local high competition for space generated by the growth pattern in the colony (such as a concave growth surface due to accelerated or more vertical growth of peripheral corallites to combat a high sediment settling rate). Increase is suppressed under these conditions of crowding, as is the growth of 'extra-large' corallites. The fact that in fig. 6b, increase in a nearby area at the same level to that in fig. 6a does occur as expected supports this conclusion. The more numerous or more continuous appearance of offsets and the occurrence of larger corallites in the same species (figs. 5a, 6c, d) reflects situations where corallites are diverging and space competition is low. The main function of 'extra-large' corallites seems to be space filling in such colonies when competition is particularly low before a period of peak increase.

Although the periodicity of the density banding and peak increase can be considered well established, the causal mechanism and timing of these events within the year are more problematical. The considerable amount of recent work on density banding in scleractinian corals relevant to these problems has been reviewed by one of us (Scrutton 1978: 156–157). Briefly, both seasonal water temperature variations (Weber *et al.* 1975a, b) and seasonal variations in light levels (Buddemeier 1974; Bud-

demeier *et al.* 1974; Stearn *et al.* 1977) have been claimed as entraining density banding and it is likely that both play a part depending on local conditions. In addition, coral growth rate has been correlated with the high nutrient levels associated with seasonal cold water upwelling (Dodge and Vaisnys 1975) and this may also influence density banding (Macintyre and Smith 1974). The timing of dense skeletal growth has been reported as in the summer (Weber *et al.* 1975a, b), the autumn (Stearn *et al.* 1977), or the winter (Knutson *et al.* 1972; Dodge and Thompson, 1974; Buddemeier and Kinzie 1975). Although difficulties have been experienced in accurately timing this event, this range of results in all or part may also be real. It is therefore difficult to draw any firm conclusions by comparison with Recent corals about the timing of the high density bands in these Silurian favositids.

There is little evidence for the nature of seasonal variations in the ancient environment, although the likely position of the English Midlands and Wales during the Silurian, about 30°S of the equator (Smith, Briden and Drewry 1973; D. H. Tarling, from the University of Newcastle upon Tyne, pers. comm. 1979), makes a pronounced climatic seasonality likely. We have considered various interpretations of our data but of the possible entraining factors, we can be more certain of a significant annual water temperature variation, with lower winter light levels, than of any influence from cold water upwellings under these circumstances. In the majority of cases, peak increase occurs at the top of, or closely following, the deposition of a dense band. It seems reasonable to speculate that the highest rate of increase might generally correlate with rising rather than falling temperature, suggesting an autumn/winter timing for dense skeletal growth. The coral illustrated in figs. 4, 6c, d becomes of particular interest in this respect as, although belonging to the same species, *Favosites multipora*, as those illustrated in figs. 5a, 6a, b, increase occurs at a different time relative to the dense bands. One possibility is that in this case density banding was entrained by different factors so that the zone of crowded tabulae was generated during the summer and peak increase, as in the other cases, occurred in the spring. In studies of living scleractinians, however, all the corals at a particular site appear to have the same timing for density banding (for example Weber *et al.* 1975b: 144). The specimens of *F. multipora* illustrated in figs. 6a, b, c, d, come from the same locality and, although they cannot be claimed as contemporaries in life, are likely to have lived under similar climatic conditions. They come, however, from different facies (reef and inter-reef) and local conditions of substrate and sedimentation were not the same. An alternative explanation is suggested by the peripheral notching and levels of sediment incorporation coincident with the top of the dense bands in the small colony from the patch reef environment (fig. 4). If the dense bands represent autumn/winter growth, the notching and sediment cover could represent material suspended and transported by winter storms. Spring growth consisted of rapid vertical growth to escape from sediment suffocation, with consequent high competition for space at the colony surface and thus the suppression of increase. With a change to more divergent growth once some relief above the substrate had been achieved, competition for space would be reduced and increase would take place.

Table 1

Data for the four colonies illustrated by frequency histograms in figs. 5 and 6, n number of corallites/colonies; \bar{x} mean; s standard deviation; \bar{x} and s in mm^2 .

a. *Favosites multipora*

(i)R50137: 6 8 12 16 18 20 22 24 28 32 40 Total

corallites	n	54	54	54	55	53	54	50	40	43	48	47	11	
		\bar{x}	1.76	1.92	2.00	2.01	1.96	1.90	2.14	2.38	2.13	1.95	1.77	1.99
	s	0.50	0.44	0.62	0.73	0.92	1.13	1.23	0.66	0.65	0.89	0.97	0.18	
corallites	n					52	42	34	39					11
						\bar{x}	2.08	2.26	2.57	2.64				
	s					0.68	0.75	0.86	0.87					0.27
										0.75	0.73			

(ii)R50138: 37 33 29 25 21 17 13 9 5 1 Total

corallites	n	61	64	55	59	66	66	69	74	71	72	10	
		\bar{x}	1.74	1.69	1.86	1.75	1.62	1.56	1.52	1.45	1.49	1.39	1.61
	s	0.40	0.53	0.28	0.29	0.35	0.36	0.26	0.25	0.30	0.37	0.15	
corallites	n	55	58										10
		\bar{x}	1.86	1.84									
	s	0.19	0.25										0.18

21 17 13 9 5 1 Total

corallites	n	58	59	57	63	56	66	6
		\bar{x}	1.89	1.87	1.81	1.68	1.78	1.56
	s	0.48	0.44	0.39	0.51	0.47	0.48	0.12
corallites	n	56	54	46	56	54	64	6
		\bar{x}	1.92	1.96	1.95	1.81	1.81	1.59
	s	0.44	0.31	0.26	0.37	0.44	0.43	0.14

(iii)R50139: 2 4 6 8 10 12 14 16 Total

corallites	n	57	56	57	61	59	55	48	48	8
		\bar{x}	1.75	1.73	1.67	1.59	1.53	1.70	1.99	2.04
	s	0.62	0.81	0.75	0.81	0.96	1.07	1.06	1.18	0.18
corallites	n	50	49	50	43	27	31	33	37	8
		\bar{x}	1.88	1.91	1.83	1.99	2.42	2.45	2.50	2.47
	s	0.53	0.67	0.65	0.60	0.59	0.80	0.87	0.99	0.30

28 30 32 34 36 38 40 42 44 46 48 Total

corallites	n	48	47	42	39	46	41	52	56	57	43	36	11
		\bar{x}	1.96	2.09	2.51	2.51	2.32	2.48	1.99	1.76	1.70	2.20	2.64
	s	0.96	1.15	1.24	1.17	1.20	1.17	0.95	0.95	1.34	1.51	1.17	0.32
corallites	n	33	33	34	30	38	36	41	22	16	24	32	11
		\bar{x}	2.46	2.64	2.92	2.92	2.66	2.74	2.29	2.67	3.52	3.35	2.92
	s	0.69	0.87	0.99	0.97	1.02	1.00	0.84	0.80	0.83	0.92	0.91	0.36

b. *Paleofavosites rugosus*

(i)R50140: 4 8 11 13 15 17 19 21 23 25 27 29 31 33 Total

corallites	n	45	50	46	45	50	52	43	43	40	39	40	45	43	43	14
		\bar{x}	2.43	2.41	2.26	2.43	2.19	2.20	2.43	2.76	2.70	2.71	2.56	2.33	2.78	2.52
	s	1.09	1.14	1.27	1.24	1.20	1.27	1.40	1.42	1.44	1.45	1.38	1.63	1.53	1.59	0.20
corallites	n	40	43	39	39	36	36	34	37	31	30	24	30	35	34	14
		\bar{x}	2.62	2.65	2.56	2.69	2.73	2.84	2.92	3.11	3.27	3.31	3.50	3.20	3.25	3.02
	s	1.00	1.05	1.15	1.13	0.95	0.97	1.13	1.21	1.08	1.08	0.92	1.28	1.29	1.39	0.30

Marginal notching and sediment incorporation, always occurring immediately above zones of crowded tabulae, are a common feature of British Wenlock favositids and have also been described by Stel (1978: 59—65) in tabulate corals from Gotland. It should be possible with further work to support the hypothesis of delayed peak increase outlined above by analysing the relative timing of increase in different areas affected and unaffected by periodic sediment cover from the same colony.

CORALLITE SIZE AS A SPECIES DISCRIMINATOR

Corallite size from section to section in these corals shows considerable variation from ontogenetic and ecophenotypic sources. Methods of selecting adult corallites only for measurement have been suggested in order to try to minimise ontogenetic effects (for example Sutton, 1966: 257). In this study, we have tried to do this by eliminating from consideration all newly appearing corallites in each section plus those first appearing in the previous section. This 'formula' is based on the shape of the hystero-ontogenetic growth curves in R50137 shown in figs. 7 and 8 but it is not necessarily valid to apply it to other corals, as we have done for illustration here. The results show that mean 'adult' corallite area thus defined, although naturally less variable in individual sections, is often more variable from section to section in any one colony than uncorrected mean corallite area (Table 1) because of the tendency for 'extra-large' corallites to balance the effect of high juvenile numbers. We have considered possible methods of minimising the effects of ecophenotypic variation on size but this can only be attempted if data such as those shown in fig. 8 are available. No simple formula seems appropriate, therefore, for standardising the calculation of mean corallite size to minimise both ontogenetic and ecophenotypic influences. In random sections of favositid colonies it is probably the best practise to calculate an uncorrected mean corallite size. Ideally, the use of corallite size as a species discriminator should be based on the analysis of intra- and intercolonial variation in large samples from well defined populations so that the extent of ontogenetic and ecophenotypic effects can be estimated.

CONCLUSIONS

1. Some colonies of *Favosites multipora* and *Paleofavosites rugosus* from the English Wenlock have a periodically dimetric appearance in serial section which is related to a fluctuating abundance of lateral offsets. A strongly dimetric appearance coincides with levels of peak increase.

2. Peak increase occurs with the same frequency as zones of close-spaced tabulae, thickened corallite walls and strongly developed septal spines (dense bands). Density banding is considered to be an annual periodicity in growth by analogy with Recent scleractinian corals. It is therefore concluded that the periodicity in increase is also an annual cycle.

3. Peak increase usually occurs at the top of or immediately following dense bands. It is considered most likely that dense bands formed in the autumn/winter and that peak increase usually occurred in the spring in these corals.

4. The abundance of new offsets depends on the intensity of competition for space at the colony surface. Competition is most intense when corallites grow convergently and least intense during markedly divergent growth. Strong space competition inhibits increase. This may result in some colonies showing delayed peak increase when sediment fouling following winter storms leads to vigorous vertical, subparallel rather than divergent spring growth.

5. The incidence and intensity of dimetrisism in these corals is therefore ecophenotypically controlled and is of no taxonomic significance.

6. Corallite area shows considerable ontogenetic and ecophenotypic variation in these corals. No simple formula seems appropriate, however, for standardising the calculation of mean corallite size to minimise these effects. The use of corallite size as a species discriminator in favositid corals should be based, therefore, on the analysis of large samples from well defined populations so that the extent of ontogenetic and ecophenotypic influences on variation can be estimated.

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