

PERIODICITY IN DEVONIAN CORAL GROWTH

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ABSTRACT. Fine growth-ridges on Middle Devonian rugose corals are seen to be grouped into regular bands of about thirty ridges up the length of the epitheca. Several hypotheses on the origin of these bands are discussed. It is concluded that the banding is most probably related to a lunar breeding periodicity and that the Middle Devonian year contained 13 lunar months each of $30\frac{1}{2}$ days.

FINE growth-ridges, of the order of 200 per cm., are to be seen on the surface of well preserved coral epithecae (Pl. 86). These features have also been termed 'striae' or 'growth-lines', but 'growth-ridges' is favoured here as the most appropriate descriptive term. Wells (1963) considers that these ridges represent diurnal increments of growth and discusses the evidence in support of this theory. By counting the ridges between annual growth-rings on fossil corals from the Devonian he obtained estimates for the number of days in the Devonian year, comparable with estimates for the same period based on astronomical data.

With the object of testing independently the results obtained by Wells, Dr. M. R. House provided some excellently preserved rugose corals from his personal collection for examination. The specimens, which represent several different genera (see Table I), are from the Potter Farm Formation and Bell Shale of the Middle Devonian in Michigan, and from the Upper Couvinian south of Trois Fontaines in Belgium, now all deposited in the Oxford University Museum collections. Also described in this paper is a specimen from the Hamilton Formation, Middle Devonian of Ontario, Canada, kindly loaned by the British Museum (Natural History).

Whilst it was found impossible to recognize yearly annulations on the material examined, it soon appeared that coral epithecae show a regular grouping of the basic growth-ridges along their length of much shorter period than a yearly increment. This grouping, briefly mentioned by Wells (1937, p. 17), is described below and its significance tentatively discussed.

In referring to these specimens the following abbreviations are used: OUM, Oxford University Museum; BM, British Museum (Natural History).

EPITHECAL CONFIGURATION

The epitheca can yield information on several aspects of a coral's life-history. Apart from the features which form the basis of this paper, the epitheca reflects some of the disturbances suffered by the polyp during life. These have an important secondary effect on the usefulness of the specimen for investigations of the growth-ridges. Very few corals are well enough preserved for the ridges to be seen in the first place, and of these, it is often only part of the epitheca that is suitable for their study.

Basically the epitheca shows a continuous vertical succession of very fine ridges, usually encircling the coral and representing successive units of growth. Each growth-ridge, in fact, represents the lip of a former calyx. Occasionally a specimen may show

where a chip in an old calyx lip has been subsequently smoothed over by the deposition of succeeding ridges (Pl. 87, fig. 4).

These fine growth increments may only extend part of the way around the circumference, usually at points where the coral has presumably been knocked or rolled from its position of growth. In order to regain the most favourable attitude for life after such a disturbance, the polyp laid down calcium carbonate preferentially on one side of the corallite, the ridges fading out and coalescing when traced around to the opposite face. Instability of the coral on the sea floor is reflected by the changes in orientation, with the consequent circumferential discontinuity of the growth increments, recorded in the epitheca (Pl. 87, fig. 2). For counting the maximum number of ridges laid down, it is obviously most useful to study those corals which have led the least disturbed life, or those that have modified their direction of growth in a constant direction (Pl. 87, fig. 3).

The possibility must also be borne in mind that if these fine growth-ridges are diurnal as it is claimed, unusual circumstances may have caused an increment to be missing for certain days, or conversely, two increments to be deposited in the same day.

Thus all ridge counts must be regarded as approximations in their interpretation, even where the curvature of the specimen presents their maximum development.

The vertical thickness of the ridges also varies, sometimes irregularly (OUM DT4), sometimes with an alternation of thicker and thinner ridges (OUM DT 5). This variation appears to be random. Often the ridges are thicker in the region of maximum growth when a change in the orientation of the calyx is involved, helping to re-establish the optimum growth position of the polyp more rapidly.

The coral epitheca also shows constrictions up its length, demarcating successive groups of ridges for which the term 'bands' is proposed. Usually the constrictions are simply deep grooves around the circumference of the epitheca, but occasionally they are emphasized by a change in the thickness of the corallite, most often being of smaller diameter above than below the groove (BM R44851). In the case of budded corals, these grooves could be matched on parent and offshoot (Pl. 87, fig. 1).

On one coral (OUM DT2), two major annulations in the form of swells could be doubtfully distinguished (Pl. 87, fig. 3). No other specimen, however, had definite indications of large period annulations disposed regularly up the length of the epitheca.

DATA

The number of ridges in each band has been counted where approximate maximum counts could be obtained. Data on ten specimens of particularly good preservation, each with a number of well-developed bands, have been summarized in Table 1. Of the ten specimens, the minimum count was twenty-seven ridges and the maximum thirty-five ridges for any one band.

The average ridge counts per band for the two specimens of *Calceola sandalina* are almost identical and slightly lower than the averages for the other eight corals. The total range of the averages, however, is only 1.1 ridges per band and the number of specimens used here does not allow any significance to be attached to slight variations within this range.

As all the specimens are from the Middle Devonian, the average of the band counts on all ten specimens, a total of 112 bands, has been calculated as representative of this

period. The degree of accuracy of this figure depends on the limited size of the sample and the order of variation with time to be expected in the number of ridges per band. To comment on the latter factor here would be to presuppose the significance of the banding. The average of a large number of counts, however, showing such a small scatter, would suggest that factors of unusual deposition or non-deposition at certain times are not important.

On some specimens (OUM DT2, Pl. 86), and on parts of others, this regular banding is very pronounced. More often it is partially obscured by intermediate, less well developed grooves. Occasionally there are more than thirty ridges between successive grooves but in these cases counts always give a multiple of about thirty ridges. For example, OUM DT6 gives one uninterrupted count of sixty-four ridges.

TABLE 1. (For explanation see text.)

<i>Specimen number</i>	<i>Number of bands</i>	<i>Average number of ridges per band</i>	<i>399/Average number of ridges per band</i>
BM R44851	12	30.9	12.91
OUM DT2	13	30.85	12.93
OUM DT3	10	30.7	12.99
OUM DT4	16	30.7	12.99
OUM DT5	12	30.4	13.12
OUM DT6	14	30.8	12.95
OUM DT7	12	31	12.87
OUM DT8	6	30.6	13.04
OUM DZ32	9	30	13.3
OUM DZ33	8	29.9	13.34
Average for ten specimens		30.59	13.04

In the case of specimen OUM DT2, the interval between the top edges of the two swells mentioned above is 401 ridges. This unit comprises thirteen bands, each on average with 30.85 ridges (Pl. 87, fig. 3).

DISCUSSION

Wells (1963) has presented the facts suggesting that the fine ridges on coral epithecae represent diurnal increments of calcium carbonate deposition. Whilst direct experimental data to confirm this hypothesis are lacking, the circumstantial evidence is nevertheless strong. The significance of the regularly repetitive banding of the coral epitheca is discussed here presuming such a time-growth relationship.

Bands per year in the Middle Devonian

Periodically, the corallite building process of the polyp was disturbed, causing a radical reduction in the deposition of calcium carbonate, reflected by a constriction in the epitheca. In the Middle Devonian this phenomenon occurred on average every 30.59 days

EXPLANATION OF PLATE 86

Part of the convex face of OUM DT2, showing six well-developed bands. The figures indicate the ridge counts between successive constrictions in the epitheca. The individual ridges are also clearly shown, $\times 20$.

during the growth of the coral. It would greatly help, in investigating the causal factor behind this periodicity, to know the length in days of the Middle Devonian year and thus establish a numerical relationship between the banding and the year.

Wells (1963, fig. 1) plots a graph of 'days in the year' against 'geological time', based on astronomical calculations and radioactive isotope age determinations for the geological systems. Between the base and the top of the Devonian system these estimates give a drop in the number of days per year from 402 to 396.

In order to calculate the number of days in the Devonian year from fossil coral material, it is necessary to determine the annual growth rate. Whilst Wells (1963, p. 950) recognizes yearly annulations on the corals he has studied, it has been concluded from the material examined here that, for these specimens at least, no regular grouping of ridges larger than the bands described above can be distinguished. The one case in which doubtful annulations occurred has already been mentioned, but even this specimen is by no means convincing.

Extrapolating, therefore, from the astronomical calculations alone, the Middle Devonian year was approximately 399 days in length. If the average band count for each of the corals in Table 1 is divided into 399 the result is a striking series of figures closely grouped about the number 13. Using the average band count for all ten corals the figure is 13.04. Thus the data strongly suggest that thirteen bands were laid down by these corals in the course of a Middle Devonian year.

Interpretation of banding

In order to interpret the banding it is necessary to seek analogy with modern corals for signs of a cyclic process which might reasonably have affected their Devonian forebears. The figure of thirteen bands per year suggests a possible connexion between the moon and coral growth. There is some evidence in support of such a connexion: Dr. S. A. Wainwright of the University of California (personal communication) has observed banding on *Lophelia pertusa* Linné, a living coral from the Norwegian fjords, on which he was also able to count the diurnal ridges. His counts approximated closely to twenty-eight days per band, the length of a present-day lunar month.

Possible ways in which the moon might affect coral growth are discussed, for convenience, under three separate heads.

1. *Tidal effect.* There is a cycle in the amplitudes of the tides with two maxima and minima, the springs and neaps respectively, occurring every lunar month. It is conceivable that for corals living close to the surface the periods of maximum amplitude might adversely affect growth by bringing the coral into highly agitated surface waters or even exposing it at low tide.

If the constrictions in the epithecae represent such tidal disturbances, then two bands would represent one lunar month and it would be concluded that the Middle Devonian year comprised $6\frac{1}{2}$ lunar months. The huge energy changes involved in converting this cycle to the present-day thirteen lunar months per year in the space of some 350 million years makes this seem highly unlikely. Moreover, the corals considered here show no indication of being adapted for life in highly agitated, near-surface waters. Specimens from the Bell Shale and Potter Farm Formation sometimes show signs of disturbances in the formation of their epithecae, but these are consistent only with occasional rolling

or toppling, most probably due to instability rather than water activity (e.g. OUM DT6). Specimen OUM DT7 shows no change at all in the orientation of its calyx during life.

2. *Variation in nutrient supply.* Dr. S. A. Wainwright, with the case of *Lophelia pertusa* in mind, suggested to the author that regular fluctuations in nutrient supplies might affect the polyp's skeleton building ability. Periods of near-starvation with a consequent lowering of the animal's energy level might sufficiently suppress calcium carbonate deposition to produce a constriction in the epitheca.

Modern corals feed on elements in the zooplankton, but there seems to be no evidence of periodic fluctuations in the abundance of these minute animals that could apply to this case. It is possible that the low spring tides could deprive the polyp of its normal food requirements if the coral lived close to the surface; but here the discussion under the previous head applies. Alternatively, the distribution in the sea of the zooplankton might be affected by moonlight. These animals are very sensitive to illumination and their level in the sea appears to be largely influenced by light intensity. It does not seem likely, however, that such a control could be sufficiently sensitive to significantly reduce the coral's nutrient supply. Hatai (1940), reporting on work done at the Palao Tropical Biological Station, states that although zooplankton is scanty in Iwayama Bay, it appears to be sufficient for luxuriant coral-reef growth. Other workers have shown that it takes a polyp several hours to digest a single animal so that their nutritive requirements in terms of plankton abundance are not very large. Thus it would require the coral environment to be virtually free of zooplankton to affect coral growth significantly.

3. *Lunar breeding periodicity.* The only other influence of lunar periodicity on the metabolism of corals generally appears to be through their breeding cycle. Many modern reef corals, and perhaps other corals whose breeding habits are not known, seem to have an approximate lunar periodicity in breeding although no reference is known to the habits of *Lophelia pertusa* in this connexion.

It is possible, however, that a periodic preoccupation with breeding in the coral metabolism could inhibit to some extent its normal function of calcium carbonate deposition. Krempf (1935) has noted a rhythmic succession of dissepimental platforms in *Favia* which he correlates with periods of sexual activity in living polyps. The two functions are connected, he suggests, by a 'mécanisme cytologique simple'. Wells (1937, p. 17), following Krempf's suggestion, equates the banding on fossil corals with periods of planulation. These he assumes to be of lunar periodicity on the basis of the relationship between the banding and annual rings on the corals he had observed.

EXPLANATION OF PLATE 87

Fig. 1. Specimen OUM DT3 showing well-developed banding (bands a, b, c, d), which can be traced from parent to young bud, $\times 4$. 2, Specimen OUM DT9, *Tabulophyllum* sp., same horizon and locality as OUM DT7 and OUM DT8. The attitudes of the irregular bands a, b, c and d reflect changing orientations of the calyx in response to toppling or rolling of the corallite, $\times 4$. 3, A side view of specimen OUM DT2 illustrating the thirteen well-developed bands on the convex face of the epitheca corresponding to the interval between the top edges of the questionable annual rings, indicated on the concave face, $\times 3.5$. 4, The repair of a chip in an old calyx lip on specimen OUM DT4. The incremental growth ridges can be clearly seen, $\times 10$.

Whilst confirmation of this relationship is lacking, it is nevertheless a possibility to be considered.

There are two types of lunar breeding periodicity known in living corals. In the first, breeding occurs twice in a lunar month. It is thought that maturation, occurring at each spring tide, is brought on by rhythmic changes in water pressure due to the tides. Korringa (1947) thinks that breeding in *Pocillopora bulbosa*, investigated by Marshall and Stephenson (1933), is of this type, although the example is complicated. In the second type, there is one breeding maximum in each lunar cycle. Here the motivating factor appears to be moonlight, with breeding usually falling between the full moon and the last quarter. Several examples of this periodicity are known from the work of Abe (1937) and Atoda (1947*a*, 1947*b*, 1951*a*, 1951*b*) at the Palao Tropical Biological Station. All four corals studied by Atoda extruded planulae with lunar periodicity all the year round.

If a lunar breeding periodicity is related to the banding seen in Devonian corals, then a single period of planulation each lunar month is the more probable situation. The alternative bi-monthly cycle would suggest that the moon encircled the earth six and a half times a year in the Middle Devonian, a situation already considered unlikely on the grounds of the large energy changes implied between that period and the present day. Thus the conclusion remains that then, as now, the moon orbited the earth thirteen times in the space of a year.

CONCLUSIONS

The regular banding observed on coral epithecae is thought to represent the effect of a natural periodic phenomenon on coral growth. On the corals studied thirteen bands were deposited in the course of a Middle Devonian year. This time-growth relationship suggests a connexion between the lunar cycle and skeleton building for which three possibilities are discussed. The most likely influence on growth appears to be through a monthly lunar breeding periodicity in the corals concerned. Acceptance of this theory leads to the conclusion that the moon circled the earth thirteen times in the course of a Middle Devonian year with a lunar cycle of $30\frac{1}{2}$ days.

Clearly a great deal more must be known about the habits of living corals before this theory can be properly evaluated. If, however, a direct analogy can be made between the banding on *Lophelia pertusa* and that on the Devonian corals, then irrespective of the exact causal mechanism involved, the conclusion is the same.

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Material. Details of the quoted specimens are as follows:

BM R44851 *Eridophyllum* sp. Hamilton Formation, Middle Devonian: south of London, Ontario, Canada.

OUM DT2 ?*Heliophyllum* sp.; OUM DT3 *Cylindrophyllum* sp.; OUM DT4 *Heliophyllum halli* Edwards and Haime; OUM DT5 *Cystiphyllodes americanum* (Edwards and Haime); OUM DT6 *Cylindrophyllum* sp., all from the Bell Shale, Traverse Group, Middle Devonian: spoil from overburden, Rogers City limestone quarry, Rogers City, Presque Isle Co., Michigan, U.S.A. OUM DT7 ?*Disphyllum* sp.; OUM DT8 *Cylindrophyllum* sp., both from shale above 'Silo Terrace', Potter Farm

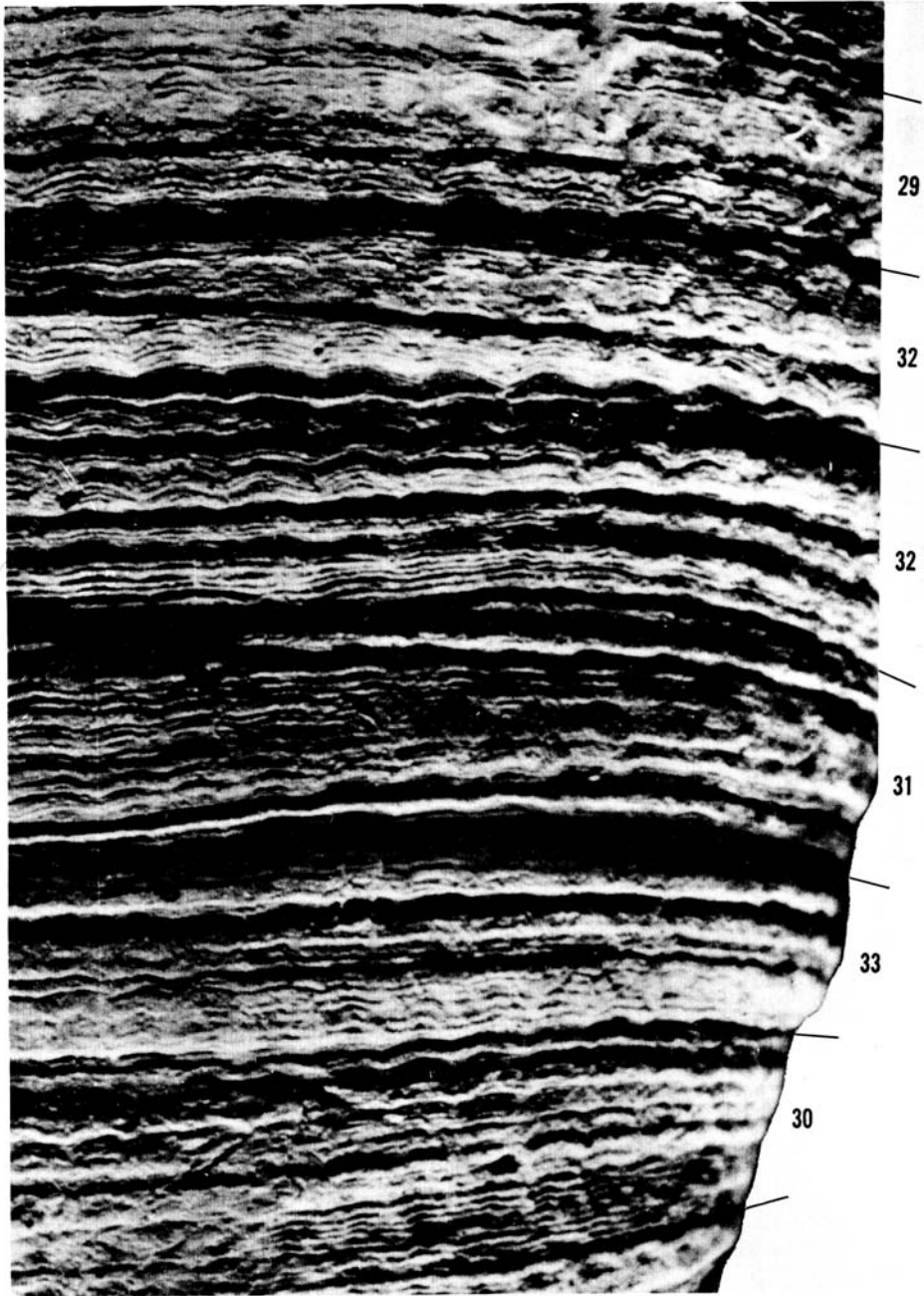
Formation, Traverse Group, Middle Devonian: small shale pit, northwest corner of Alpena (Evergreen) Cemetery, south-west quarter, sec. 21, T. 31 N., R. 8 E., near Alpena City, Michigan, U.S.A. OUM DZ32 and OUM DZ33 both *Calceola sandalina* (Linné), Upper Couvinian calcareous slates, Middle Devonian; south of Trois Fontaines, Belgium. All OUM specimens collected by Dr. M. R. House.

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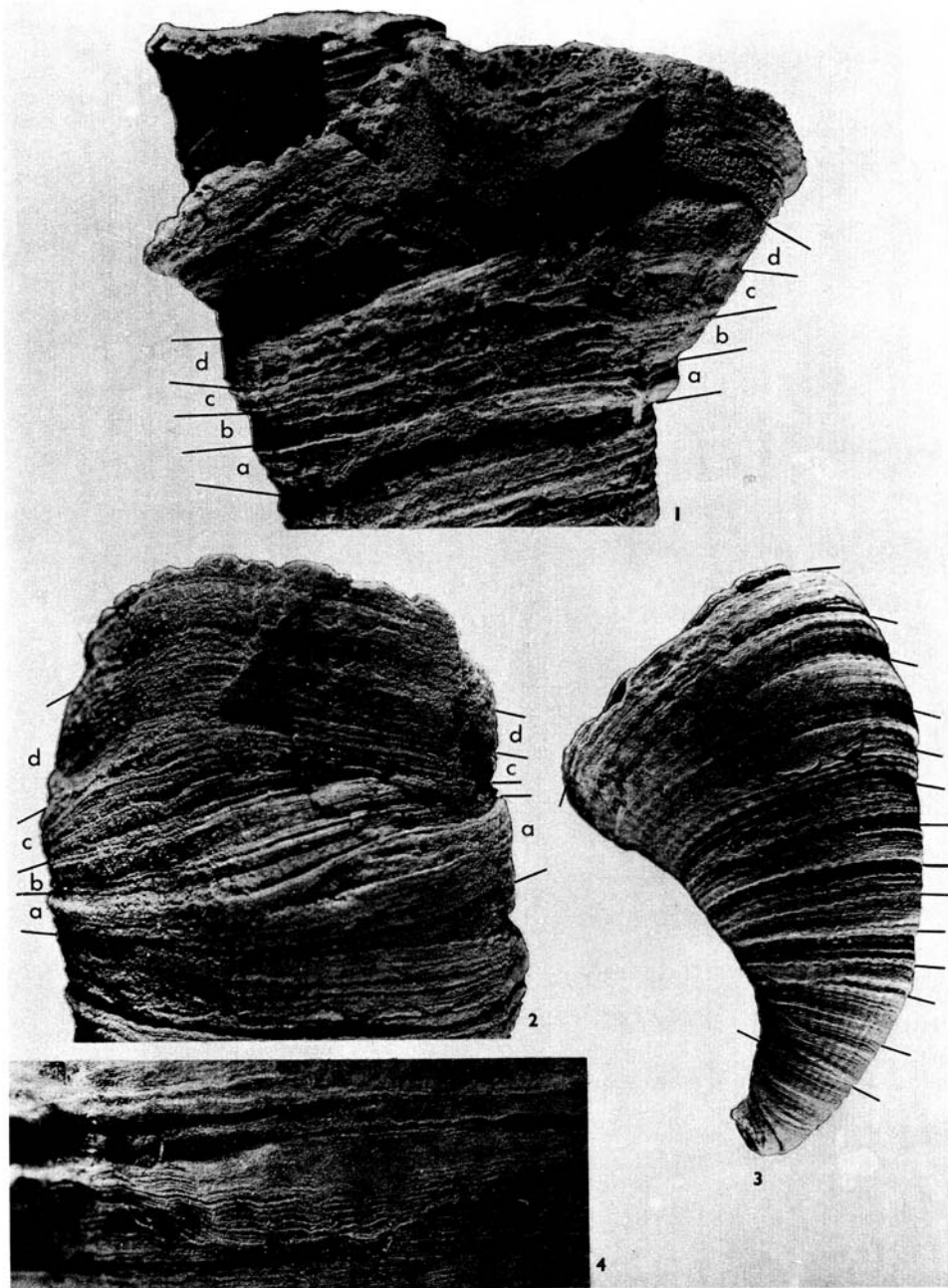
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