A COMPUTER MODEL FOR SKELETAL GROWTH OF STROMATOPOROIDS

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ABSTRACT. A robust and versatile computer model of simple accretionary laminar growth can be developed based on probabilistic accretion of pixels on a raster array. The model is a reasonable analogue for growth of simple organisms such as stromatoporoids. Experiments with the model allow the effects of sedimentation and various alternative growth algorithms to be simulated. The model can be validated, with some reservations, on theoretical and empirical bases: the simulations show similarities to observed stromatoporoid morphologies. The results suggest that morphology is strongly influenced by the pattern of sedimentation and that stromatoporoids required a local pause in sedimentation in order to become established. The results are consistent with the view that stromatoporoids were integrated organisms but with a low level of organization allowing a degree of autonomy of modular growth.

FOSSIL stromatoporoids were sponges which secreted a secondary calcareous skeleton within a soft tissue coating. Similar modern sponges reveal that soft tissue is limited to the upper few millimetres of the skeleton; as the sponge grows, the underlying skeleton is vacated (Hartman and Goreau 1970; Stearn 1972, 1975). The final result is a laminated skeleton which can display a range of growth geometries. This study presents a computer-based model to simulate skeletal growth in stromatoporoids, and demonstrates significant parallels between real and simulated forms. The model allows exploration of the controls on growth of stromatoporoids and assists palaeoecological analysis of these fossils.

The term 'stromatoporoid' refers to a particular organization of skeletal structure, typically comprising sheet-like lateral elements (laminae) and vertical rod-like elements (pillars) arranged as a reticulum. Stromatoporoids are traditionally regarded as a taxonomic unit within the Porifera (Stearn 1975), but more recent views are that the stromatoporoid structure represents a grade of organization of sponge skeletons unrelated to taxonomy (Vacelet 1985); Wood (1990) recognized four grades in sponges, with some degree of overlap.

These conflicting views of the status of stromatoporoid structure are not relevant to the morphological computer simulations presented here, but two skeletal structures amongst sponges generate remarkably similar external shapes: stromatoporoid and chaetetid. Chaetetids differ from stromatoporoids in being composed of small tubes. In both cases, the morphology is well documented and both exist as skeletons containing growth lines, so that the skeleton can be considered as an accreted pile of laminar units. The shape of successive laminae may change through growth, such that the overall result may vary from a flat sheet to a column. Sponges are modular rather than colonial organisms, and therefore it is appropriate to refer to each sponge as an individual rather than a colony. Coloniality in sponges is therefore truly at the cellular level. Wood *et al.* (1992), drawing on work by Jackson (1983) and others, discussed the relationship between modularity and growth success in sponges, and concluded that highly modular organisms live long lives and grow to large sizes, and can therefore be successful at activities such as reef building.

Earlier works use the term coenosteum to describe a single stromatoporoid; coenosteum derives from hydrozoan coelenterate terminology, from the days when stromatoporoids were generally considered as hydrozoa. The term coenosteum should now be abandoned in stromatoporoid terminology (Stearn 1984, p. 316).

There have been a number of attempts at understanding the morphology of stromatoporoids and related organisms. Kershaw and Riding (1978, 1980) illustrated field geometries of most stromatoporoids using triangular arrays, and a similar approach was applied to corals by Young and Scrutton (1991). Kershaw and West (1991) discussed the geometry of laminar growth for chaetetids and noted that such an approach could be applied to other calcareous skeletal organisms, such as trepostome bryozoans (Ross 1987) and tabulate corals. The use of computer simulation is a new initiative in this field.

COMPUTER MODELLING OF SKELETAL GROWTH

Computer models are often based on equations which describe the processes in the system: the equations may be derived empirically or from theoretical considerations. This is the approach used, for example, to model growth of molluscan shells by Raup (1966), of stromatoporoids by Hofmann (1969), of corals by Graus and Macintyre (1976), and to model accumulation of reef carbonates by Bosence and Waltham (1990). Such mathematical models could, in principle, be devised for accretionary systems. To cite mundane examples, the formation of hailstones (or lapilli) by accretion in a cloud, or of ooliths in agitated shallow seas, could be modelled by the equation for a sphere with successively increasing radii, and this could be extended to constructing half-spheres to emulate accretion around a nucleus on the sea bed. This mathematical modelling approach has been rejected for the present context for two main reasons. Firstly, any equation that might be used could not be regarded as in any way inherent in the organism; it would not emulate genetic programming (blue-green algae do not make ooliths because they are genetically programmed with the equation of a sphere). Secondly, apart from very simple situations, the dynamic and probabilistic aspects of growth become too complex for mathematical models.

An alternative approach is to devise simple rules which can be applied to any point on the simulated organism. These can be sufficiently simple and general that they can readily be regarded as a result of genetic control, basic physiological response or external physical effects. In practice, it is convenient to construct the simulated organism on a grid or raster, which can be directly represented on the pixel array of the computer screen. Consequently, the rules for accretion are designed to be applicable to each pixel in the raster array. This approach allows each small part of the simulated organism to operate autonomously, with no central control imposed by the organism as an integral unit. This is in contrast to the mathematical modelling approach, in which exact control of all parts of the organism is implied by the use of an equation. Indeed, success at modelling an organism using the raster approach may have implications about the level of organisation of the organism.

DEVELOPMENT OF A MODEL FOR STROMATOPOROID GROWTH

Accretion on a raster array

Accretionary growth simply involves the addition of new material on existing surfaces; usually surfaces that have resulted from previous increments of accretion. In terms of the computer model, accretion involves 'switching on' only these pixels which are immediately adjacent to already 'switched on' pixels. However, although the raster array is a convenient way of accounting for occupation of space, it is unnatural in that; (1) each raster cell or pixel is a quantum which bears no relation in size, shape or position to the units of accretion in the real organism (which may be biological cells or even molecules): it is computationally awkward to account for fractions of pixels; (2) the raster imposes an artificial square anisotropy on the model.

The effect of these problems can be demonstrated by considering accretion around a simple one cell nucleus (Text-fig. 1A). If all neighbouring cells are 'switched on', over several increments we

TEXT-FIG. 1. Accretion on a square array or raster of pixels. A, deterministic accretion, producing a result that reflects the square anisotropy of the raster. B, stochastic accretion, where the accretion of a pixel is never certain; probabilities can be fixed so that the structure accretes at the same rate in all directions.
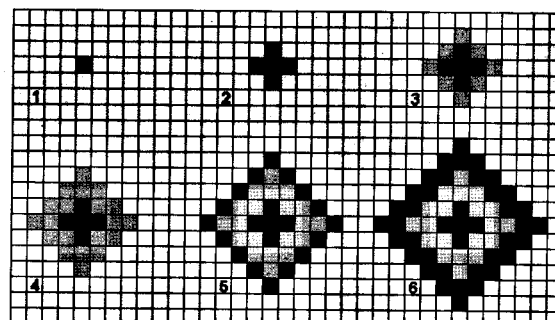
A
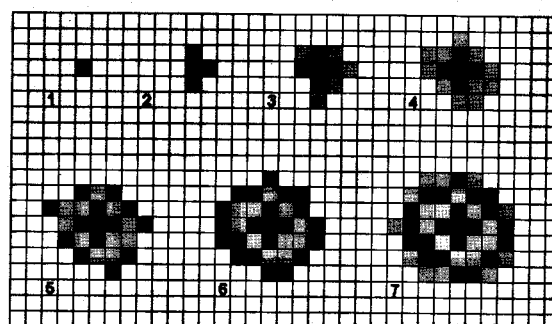
B

accumulate a structure with square symmetry, rather like a crystal but not like organic accretionary structures. This is because accretion of one cell in the direction of the 45° diagonals requires accretion of one horizontal and one vertical increment, so these directions are more slowly extended. The square anisotropy creates the problem, and the idea of pixels as quanta prevents the solution of the problem by use of fractional pixel accretion (e.g. fill two-thirds of a diagonal pixel for each horizontal or vertical increment).

The problem can be solved by probabilistic accretion. In this scheme, pixels are never certain to be accreted to the structure; we attach probabilities of accretion to all candidate pixels, where the probabilities are determined by various aspects of spatial location. This, as we shall demonstrate, is the crucial aspect that confers great flexibility and robustness to the model. We can devise rules for determining the probabilities to be attached to candidate pixels on the basis of spatial disposition, such that these are analogous to the varying growth rates of different parts of a real organism.

The problem with the 45° diagonal pixels is that 2 increments of purely horizontal or vertical accretion extend the structure 2 units in those directions, but diagonal accretion in 2 increments (1 horizontal and 1 vertical) extend the structure only $\sqrt{2}$ units. So, the rate of diagonal accretion needs to be enhanced relative to the vertical or horizontal rates. In a probabilistic model, this can be done by increasing the likelihood of 'switching on' a pixel if it has two rather than one 'switched on' neighbours (Text-fig. 1B).

Description of basic model

The initial state of the basic model is a flat sediment surface and a single pixel 'seed' for the structure. Pixels not occupied by the simulated organism are coded zero; the structure is made of pixels with non-zero pixel colour codes. In each increment, adjacent pixels are scanned and are allocated probabilities of becoming non-zero ('switched on') according to position.

If there are no non-zero pixels amongst the four immediate neighbours, or if the position is occupied by sediment, the probability P is zero. If there are n non-zero pixels amongst the four immediate neighbours and the position is not occupied by sediment, the probability P is:

$$P = \frac{n}{n+1}.$$ (1)

The status of a pixel is decided as follows: a random number is generated in the range 0 to 1; if the random number does not exceed P, the pixel becomes non-zero; otherwise it remains 'off'. In practice, this algorithm is found to create good approximations to circles and semicircles in simple accreting systems. The result of the simplest type of run of the algorithm is shown in Text-figure 2.

TEXT-FIG. 2. Simulation resulting from the basic model for accretion around a single-pixel nucleus on a sediment surface. In this and subsequent simulations, there are about 4 pixels per millimetre.

In order to show the shape of successive increments of accretion, the non-zero pixels are allocated alternating colour codes (black and stippled on hard-copy) after every fixed number of iterations (eight in the simulations presented here).

The basic model can be adapted to incorporate the effects of various factors by incorporating more complex rules for calculating pixel probabilities.

Geotropism

Geotropism is a very common attribute of organisms; negative geotropism (preferentially growing upwards) is likely to be useful for moving clear of turbid sediment or competition, and closer to light. This is difficult to distinguish from positive phototropism (see Graus and Macintyre 1976), which may have the same purpose and effect; these are not distinguished in the versions of the model presented here. Geotropism is incorporated into the model by introducing a different probability-weighting to pixels with vertically disposed non-zero neighbours. A geotropic factor '*geo*' is specified by the user. If the candidate pixel is immediately above a non-zero pixel and has no other non-zero neighbours, its probability of being accredited is:

$$P = \frac{geo}{geo+1}.$$ (2)

(Compare with equation 1). If the candidate pixel is immediately lateral to a non-zero pixel and has no other non-zero neighbours, its probability of being accreted is:

$$P = \frac{1/geo}{(1/geo)+1}.$$ (3)

Consequently, the probability is enhanced if there is a non-zero pixel below, but reduced for every lateral non-zero pixel. Values of *geo* greater than 1 result in more rapid vertical growth; *geo* less than 1 inhibits vertical growth (Text-fig. 3).

Effect of sedimentation

As noted above, no pixel is accreted onto the structure if it is in a position occupied by sediment. This has a mundane consequence if the sediment surface remains constant, but this is unrealistic. Stromatoporoids are at least sometimes associated with significant sedimentation rates and we
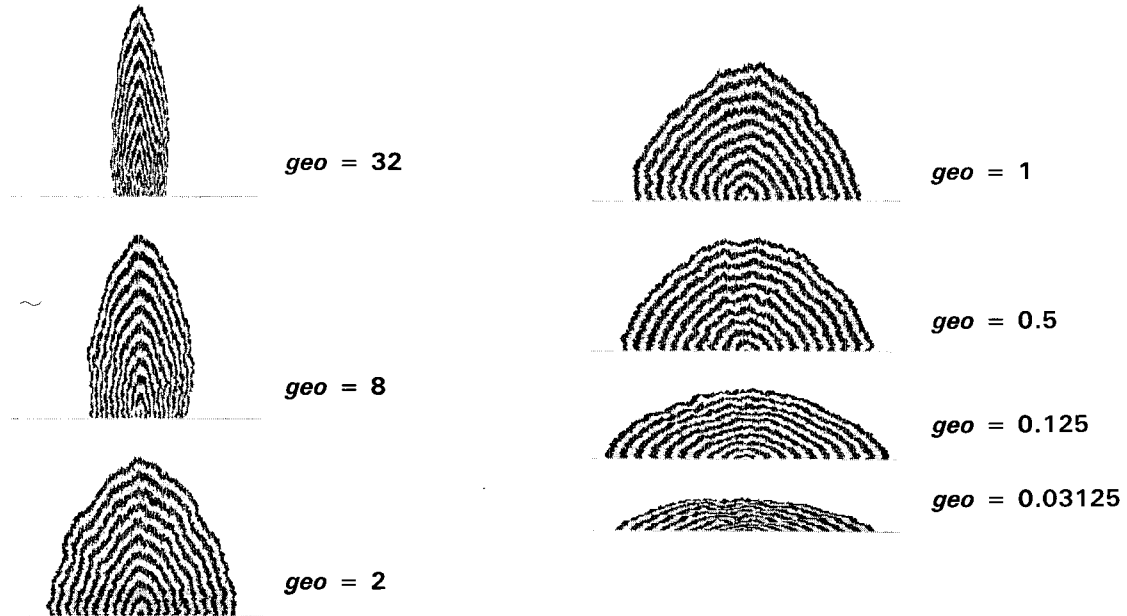
TEXT-FIG. 3. Simple accretionary structures with varying value of the geotropism factor *geo*.

expect sediment accumulation to affect the growth of the structure. In the computer model, only those pixels above the sediment surface are scanned as candidates for accretion, so a vertical addition to the surface position will automatically simulate smothering of growth sites by sediment cover. The sediment surface could be controlled manually after each iteration of the program, but experiments with the model have focused on the alteration of three sedimentation parameters: (1) interval between sediment increments (units: number of iterations of accretion algorithm); (2) amount of sediment in each increment (units: pixels); and (3) length of hiatus during initial establishment of structure (units: number of iterations of accretion algorithm).

Experimental simulations can be run to demonstrate the effect of each parameter. This is best shown by means of an array of simulations on a 2-dimensional space defined by: (1) interval between sediment increments; and (2) ratio of amount of sediment in each increment to the interval between sediment increments. Such an array is shown for the simple accretionary model in Text-figure 4 and demonstrates the following properties.

(1) The partial occlusion of the accreting surface by sedimentation, followed by growth back over the sediment surface during quiescent intervals, results (predictably) in a ragged lateral edge to the structure. This property was quantified using a raggedness index by Kershaw (1984).

(2) Where sedimentation is significant and consistent, the bases of structures have a clear conical geometry.

(3) Once established in a regime of regular sedimentation, structures grow indefinitely.

(4) The occupancy of the 2-dimensional parameter space, and hence the diversity of geometries, is constrained by the condition where sedimentation rate exceeds growth rate.

As we shall see, points (2), (3) and (4) are not compatible with observations of real stromatoporoids. The range of possibilities can, however, be extended by using the third parameter cited above (allowing a hiatus in sedimentation). Using a hiatus of 100 units, a comparable array of forms can be generated (Text-fig. 5), including high-domed morphologies with on-lap of laminae.
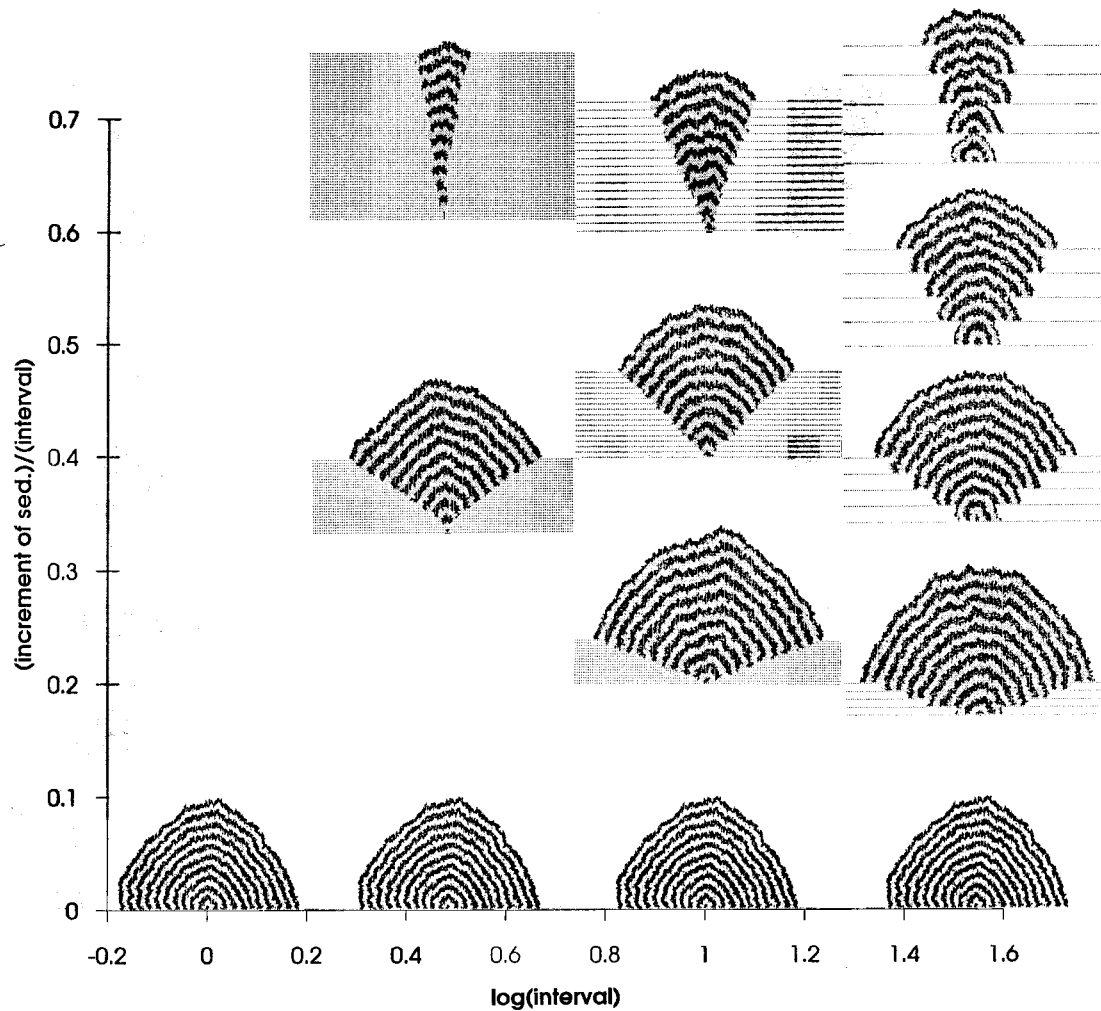
TEXT-FIG. 4. Array of simulations with varying interval between sediment increments and amount of sediment in each increment. Horizontal dotted lines show successive positions of sediment surface. The forms shown at the top of the array represent the highest values of relative sedimentation rate at which structures can develop. Above this, the fundamental constraint of average sedimentation rate exceeding average growth rate applies; in this region the structures are extinguished soon after initiation. Also, note the prevalence of conical bases and ragged edges.

Response to sediment surface

The basic model includes rules which regard the sediment surface as neutral; probabilities attached to pixels adjacent to sediment are not enhanced or reduced. However, it is conceivable that proximity to sediment could either inhibit growth (see section on competition below) or enhance growth. The positive effect is introduced by a modification of the basic model, allowing sediment to have a similar effect as the pre-existing accreted structure in influencing the probability of inclusion of new pixels. The probability calculation $P = n/(n+1)$ (equation 1) is applied with the specification that n is the number of non-zero adjacent pixels, including those with sediment colour codes, but with the proviso that one of the n must belong to the accreting structure. This assures
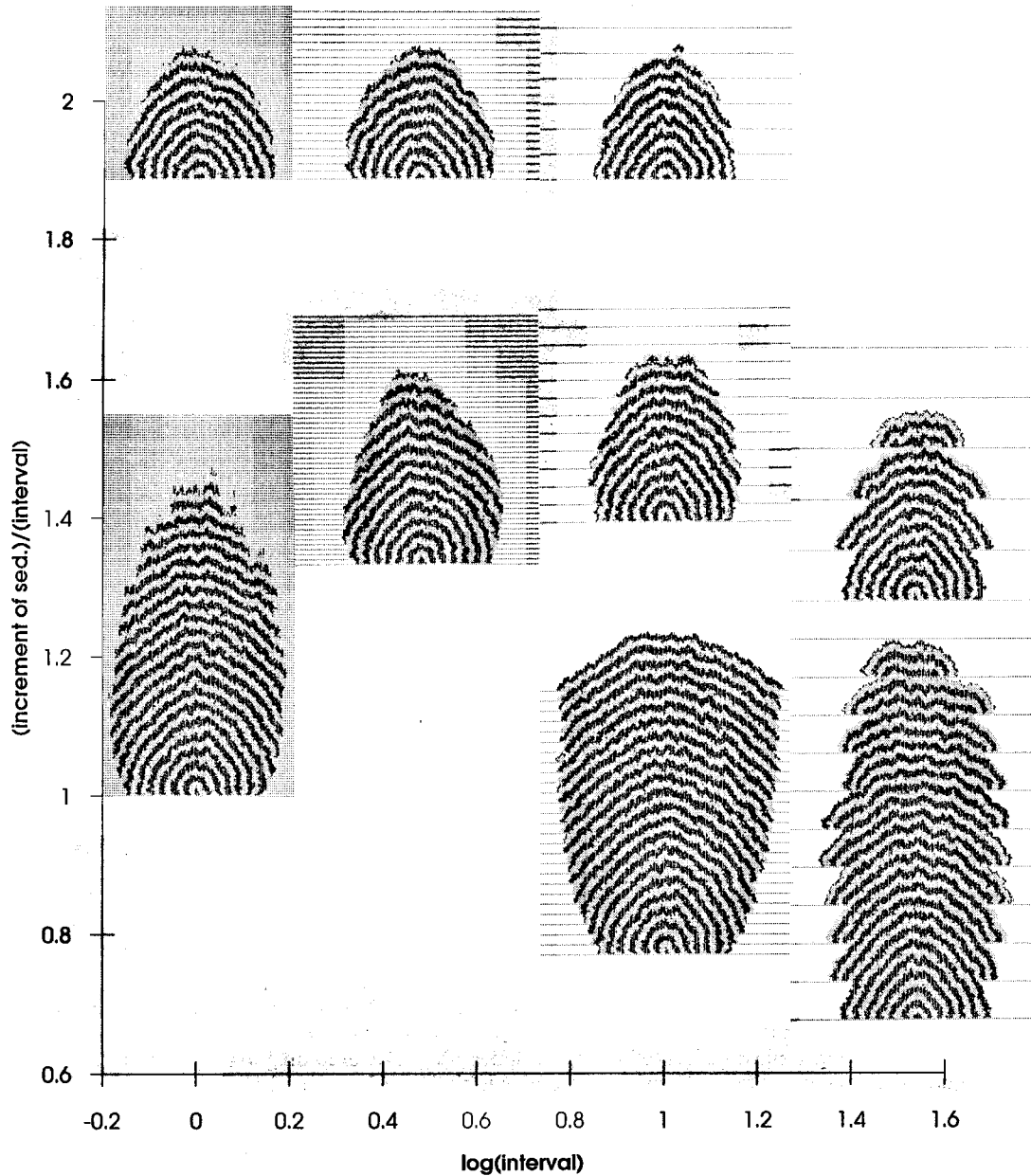
TEXT-FIG. 5. Array of simulations similar to that shown in Text-figure 4, except that structures are permitted to become established during a hiatus of 100 units. Most structures are eventually over-run by sedimentation, but this array includes different geometries, typically with on-lap of laminae. Geometries with lower relative sedimentation rates are possible; these are similar to those in Text-figure 4, but broader.

that structures do not nucleate arbitrarily across the whole sediment surface. There is an analogous modification to equation 2 if the *geo* factor is used. These modifications produce structures with broader bases (Text-fig. 6A), which may be advantageous for stability and for excluding spatial competitors.

TEXT-FIG. 6. A, structure produced by modified model in which contact with sediment has a positive effect on accretion. B, merging of structures modelled by application of the basic model to an initial state where there are two 'seeds'.

Merging of multiple colonies

The algorithms described above can be equally well applied to initial states in which there are two or more 'seeds'. In the simple versions of the program, there is no sense of individual identity of pixels or structures, so separate structures merge together. Further increments have the effect of masking the original separate structures (Text-fig. 6B).

Competition

The simple algorithms so far described treat pixels equally, regardless of general position on the developing structure. This could be regarded as unrealistic; for example, positions projecting on the top of the structure may be better favoured for access to food or oxygen, when compared with positions in crevices or adjacent to the sediment. This may have a number of different types of result, depending on the level of organization of the organism.

(1) If local parts of the structure are highly autonomous, they will compete with each other and favoured parts of the structure may grow at the expense of others.

(2) If resources are to some extent distributed, growth may be equal regardless of site.

(3) If growth is highly centrally organized, there may be strategies of: (a) enhanced growth at favoured locations to take advantage of resources; or (b) systematic patterns of growth determined by other criteria (e.g. structural strength). There may be genetic control of growth form underlying such strategies (Kershaw 1990).

The basic model described in previous sections is based on type 2. A model for type 1 will now be described, the results of which may be indistinguishable from those of type 3a. Type 3b is, however, beyond the scope of the current suite of models.

If pixels are autonomous, we can model a situation in which pixels are more likely to form sites of accretion if they are in favoured positions. Positive feedback in growth can be achieved if pixels in more open projecting positions are favoured over those in enclosed positions; this is intuitively reasonable. The 'openness' of the position is assessed by the modified program by counting the number of non-zero pixels from a circular scan of 16 points at a given radius from the candidate pixel and at 22·5° intervals. The number of the 16 that are occupied by the structure or sediment
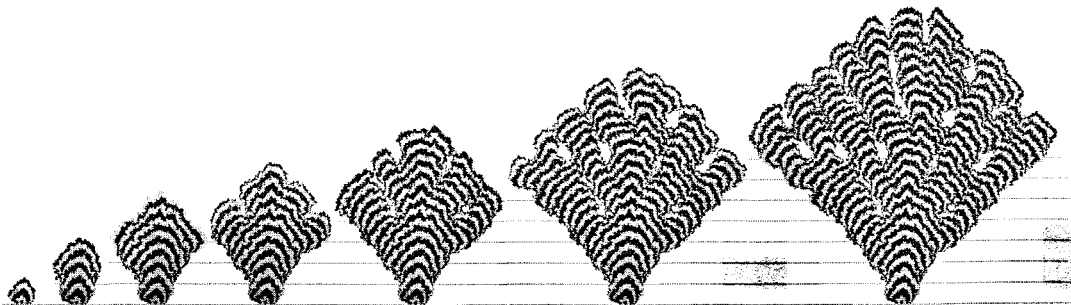
TEXT-FIG. 7. Stages of growth of a structure using a model with local autonomy and competition. Accretion is enhanced at more open sites and inhibited at enclosed sites.

may be symbolized by R; the revised probability to be attached to the candidate pixel P' is then calculated from the probability P (from equations 1–3) by:

$$P' = P^{R/8}. \tag{4}$$

Consequently, positions on flat surfaces ($R = 8$) have unaffected neutral growth rates but open sites ($R < 8$) give increased growth (higher P) and enclosed sites ($R > 8$) are inhibited (lower P). The result of this algorithm (Text-fig. 7) is to enhance arbitrary local projections into major lobate branches; this can be allowed to develop into a dendritic structure. The width of the branches is determined by the specified scan radius, representing the range around a point on the organism within which the spatial arrangement of the structure has some influence.

Competition between multiple colonies

If the 'competition' algorithm described above is applied to multiply-seeded structures, they do not merge. Growth is inhibited when it takes a structure to within the specified radius of a rival structure. Smooth sided structures result (Text-fig. 8). In the case of local autonomy of growth, this result should be associated with lobate branching elsewhere on the structure. In the case of distributed growth (types 2 and 3 above), these two effects will not necessarily be associated.

TEXT-FIG. 8. Simulation of effect of two structures on each other when growth is inhibited at enclosed sites.
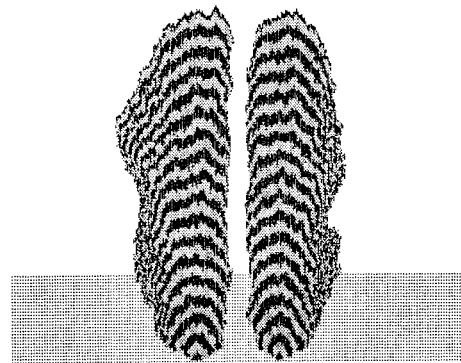
VALIDATION

The validation of computer models is always problematical. It is based on two principles: (1) assessment of processes and parameters; (2) comparison of simulations with reality.

Processes and parameters

The process involved here is accretionary growth; the parameters are the variables which control the rates and sites of growth. Many computer models are able to incorporate calibration of parameter values by using empirical data from recent analogues: thus Bosence and Waltham (1990) were able to include real rates of growth in their coral reef model. In the present study, there are no reliable sources for such information; attempts to relate growth banding to growth rate have required basic assumptions, such as Meyer's (1981) study where annual increments were assumed. Calibration on this basis can be done but does not provide unequivocal data on growth rates. We can, nevertheless, appraise the pertinence of the processes in the model in relation to apparent growth mechanisms of fossil organisms.

The raster accretion method of this study treats a skeleton as composed of minute, equal-sized units (pixels), and therefore ignores the complexities of skeletal differentiation between the various groups of taxa with similar gross morphotypes. Its application to growth of organisms with

relatively low modular integration, such as favositid corals, may not be so satisfactory, but when applied to highly integrated skeletons such as many sponges, the model may be closer to reality.

Laminar accretionary growth provides a useful concept for visualizing the overall geometric development of a skeleton of these organisms, but does not provide a means for modelling the growth mechanism. Such growth assumes that accretion took place simultaneously across the skeleton surface, but examples of stromatoporoids occur for which this was demonstrably not the case, so this concept is only partially applicable. Also, laminar growth units are recognizable as geometric entities in a wide range of phyla with different skeletal organizations, and are a reflection of the need for growth. However, they give no information about intrinsic controls in individual phyla. Laminar growth occurs in organisms with obvious differences in skeletal organization in clonal organisms (Jackson 1983), and especially in terms of the degree of integration, or modularity—a crucial concept in studies of clonal organisms. In tabulate corals such as *Favosites* a module is clearly identifiable as a single corallite, whereas in sponges modules are not so easily recognized because there are no identifiable individuals. However, because sponges filter-feed, they consist of tissue arranged in an incurrent–excurrent system. In stromatoporoids, the centres of excurrent flow are astrorhizae (sets of branching root-like grooves on the upper surface of many species). These are often arranged in an evenly-spaced pattern on stromatoporoid surfaces, so that water is drawn in through the tissue around the astrorhizae, and waste water is channelled to the astrorhizal centre and expelled (LaBarbera and Boyajian 1991). Astrorhizae therefore provide evidence of aquiferous units with unclear boundaries, which could be regarded as the closest approximation to individuals in sponges. Apart from this, sponges only show individuality at the cellular level, not recognizable in fossils. Unfortunately, not all stromatoporoids show astrorhizae, so the aquiferous limit is not a universally quantifiable feature. Using a modular approach, it is clear that in the wide variety of organisms with laminar accretionary growth, modules have different sizes and types. Modelling the growth of such a disparate array of skeletal constructions may therefore require variety of approach.

Stromatoporoid skeletal structure varies from organizations with prominent laminae to those with prominent pillars, and as a result there are no definable subunits of growth which can be recognized in all stromatoporoids, unlike tabulates or even chaetetids which have tubes as the smallest unit of growth. Consequently, growth was presumably quite locally organized in stromatoporoids (Wood 1991). Therefore the raster approach adopted here appears to be closer to the way stromatoporoids grew than for the other groups.

Within the sponges, stromatoporoids and chaetetids do not show uniform growth. Kershaw and West (1991) showed considerable internal complexity in calicle distribution in chaetetids within single individuals. In stromatoporoids, variation of internal skeletal elements occurs where parts of an individual display prominent laminae while others show prominent pillars, and some stromatoporoids show phases of growth (Stearn 1989). Stromatoporoids may show these variations on a rhythmic basis, which suggests an environmental control on the growth of successive layers of skeleton. Modelling using the raster approach adopted here is unlikely to resolve such fine scale variation. Furthermore, the stochastic nature of the computer model has no analogue in growth of real organisms: it is used as a convenient means of emulating curved increments of accretion on the raster array of the computer device. It is clear that the application here is an algorithmic approximation of real growth. Thus it does not explain how growth occurs, but is a proxy for demonstrating the geometry of growth in a skeleton. However, the basic processes of the model such as accretion on 'live' surfaces and smothering by sediment are highly plausible as properties of real organisms and have crucial influence on the final geometry of the structure.

Comparison with real forms

The simulations presented in Text-figures 4 and 5 demonstrate the dependence of shape on sedimentation. This is shown, for convenience, only for cases of regular sedimentation increments and intervals. The morphology of real forms will be determined by the effectively arbitrary history

of sedimentation and other real events. Furthermore, the shape of the initial substrate often differs from the flat geometry of the simulations. Consequently, we do not expect an exact fit of a simulation to any particular stromatoporoid specimen; rather, we should compare types and ranges of geometry.

Correspondences. There appears to be a correspondence between simulations and real forms in the following aspects.

(1) *General morphology.* The simulations generally produce types of massive domed structure, corresponding to the typical stromatoporoid morphology. This is not entirely a mundane observation; it is an important aspect of stromatoporoid morphology that more complex structures are not as typical as they are of other groups, such as corals. The special modifications that can be made to the algorithm to produce more complex structures may be analogous to the more complex growth strategies of other organisms and atypical stromatoporoids.

(2) *Geotropism.* The range of geometries resulting from changes to the geotropism factor (Text-fig. 3) match the range of degrees of convexity of real stromatoporoids (Text-fig. 9), described by
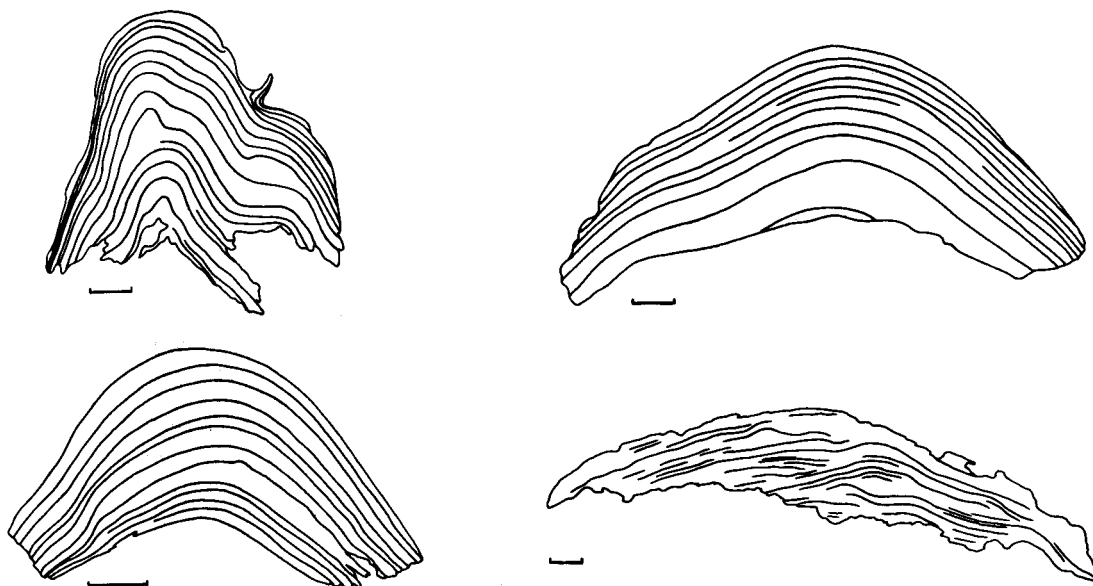

TEXT-FIG. 9. Examples of contrasting stromatoporoid geometries that can be modelled by varying values of the geotropism factor (see Text-figure 3). Notice also the concave bases, suggesting establishment on convex local highs on the substrate. All are traced from photographs of specimens from Silurian of Gotland. Scale bars represent 10 mm.

the continuum from laminar to low domical to extended domical morphotypes by Kershaw and Riding (1978).

(3) *Ragged edges.* The ragged lateral margins resulting from simulations involving periodic sedimentation (Text-figs 4–5) have the same form and the same inferred cause as those in real stromatoporoids and chaetetids (Text-fig. 10), as documented by Kershaw and Riding (1978) and Kershaw and West (1991).

(4) *Smooth margins.* Kershaw and Riding (1978) identified an 'extended domical' morphotype with smooth margins created by non-enveloping laminae (Text-fig. 11). This can be modelled by

100mm
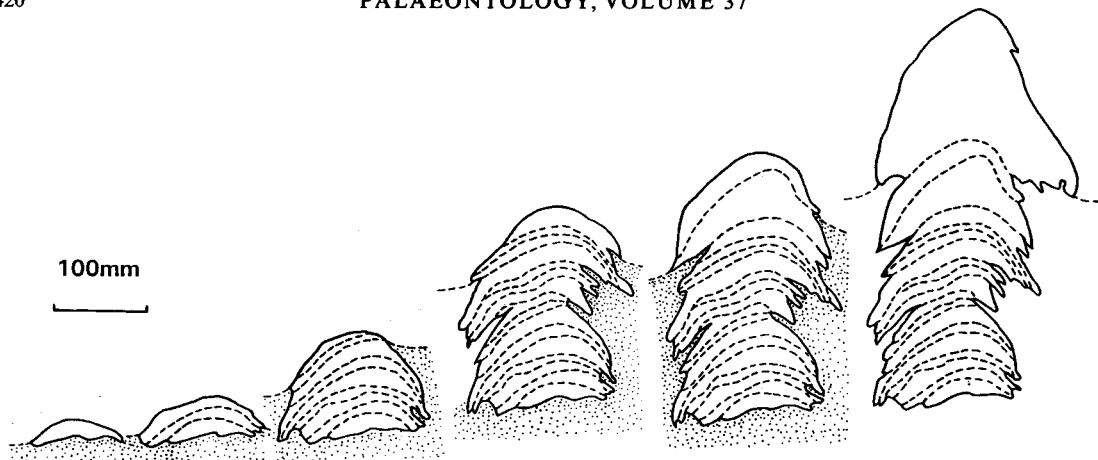
TEXT-FIG. 10. A chaetetid with sediment-induced ragged margins (from Kershaw and West, 1991, which compare with forms modelled in Text-figures 4 and 5.

frequent, small sediment increments (e.g. forms in top left of Text-fig. 5), or by interference with other individuals (Text-fig. 8).

(5) *Bulbous versus pyramidal forms*. Variation between generally pyramidal forms with broad bases, and bulbous forms with relatively narrow bases, was documented by Kershaw and Riding (1978). This variation can be modelled by varying the response to the sediment surface (compare Text-fig. 6A, 7).

(6) *Importance of hiatus*. A comparison of Text-figures 4 and 5 demonstrates the importance of an initial hiatus in sedimentation to permit growth. This is supported by the almost ubiquitous observation of flat or concave bases of real stromatoporoids (see examples in Text-figs 9, 11): the conical (convex-down) bases simulated in Text-figure 4 are rare or absent in stromatoporoids, though common in corals. Furthermore, the prevalence of concave bases in stromatoporoids suggests establishment on convexities (local highs) on the substrate, which would be sites of less local sedimentation.
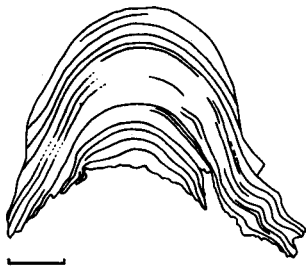
TEXT-FIG. 11. An extended domical stromatoporoid, with non-overlapping laminae (traced from photograph of specimen from the Silurian of Gotland). Compare with forms shown in Text-figures 5 and 9. Scale bar represents 10 mm.

These six points of similarity allow the basic computer model to simulate most of the range of observed morphologies described by Kershaw and Riding (1978; see, for example, their fig. 10). It should prove possible to modify and control the computer model to simulate specific complex fossils, and thus help improve understanding of an individual's growth mode and history.

Discrepancies. The following points of discrepancy between simulations and real forms suggest that we should retain some reservations about the total applicability of the model.

(1) *Some morphotypes are not realistically simulatable*. The dendroid stromatoporoids do not have the same geometry as those created by the model, as shown in Text-figure 7. The extended domical morphotype with smooth margins and non-enveloping laminae has been simulated in two ways (see point (4) above), but field evidence leaves some doubt as to whether real structures of this

type can be attributed either to continuous sedimentation or to interference with adjacent structures.

(2) *Some simulations are unrealistic.* It is a prediction of the basic model that many stromatoporoids should have conical bases (Text-fig. 4), but these are rare in nature. As noted above, the style of branching shown in Text-figure 7 is not represented in stromatoporoids, although it is reminiscent of other organic forms. It is also possible that the modification of the model that incorporates autonomous competition is not supportable as a stromatoporoid analogue.

IMPLICATIONS FOR THE INTERPRETATION OF STROMATOPOROIDS

Growth rate versus sedimentation rate

The results of the model confirm the interpretations of fossil morphologies as highly dependent on sedimentation, particularly its rate and episodicity. The model also gives some idea of the relative tolerance limits of stromatoporoids to sedimentation. An interesting and unexpected result in some simulations (Text-fig. 5) was the manner in which growing stromatoporoids were initially able to keep pace with sedimentation, but eventually become rather abruptly smothered, despite the consistent pattern of sedimentation. A non-linear and apparently complex growth history can therefore have a simple cause. However, sedimentation episodes will in reality have been variable in frequency and amount, and stromatoporoid growth cannot be assumed to have been constant, so survivorship of stromatoporoids under conditions of episodic sedimentation is likely to have been haphazard.   ⟍

Establishment of structures

We have observed that the model involving an initial hiatus (Text-fig. 5) produces more realistic results than that involving no hiatus (Text-fig. 4). Indeed, the development of many typical morphologies seems to be dependent on average sedimentation rate exceeding growth rate—a terminal condition for which the initial hiatus is essential if the structures are to develop at all. There are two possible interpretations of this.

(1) Stromatoporoid growth may have been genuinely slow and unable to keep pace with typical increments of sediment, so individuals would be immediately smothered unless they were 'seeded' on sites experiencing (for a period of time) near zero sedimentation. It is worth emphasizing that, in this model, any stromatoporoid that successfully began growth while there was *any* sedimentation would show signs of a conical base; the general rarity of these would specifically imply that the initial hiatus was essential.

(2) The 'hiatus' may be only apparent and relative; there may be an initial rapid growth phase, exceeding sedimentation rates, to allow the establishment of the structure. The lack of fossils having the geometries simulated in Text-figure 4 would therefore be due to inadequacy of the basic model of growth.

These alternatives are difficult to appraise; the observation of concave bases (convexities of substrate) perhaps favours the former.

Level of skeletal integration

The comparability of simulations to fossil material suggests that stromatoporoids, and probably also chaetetids, had some of the organizational attributes of the computer algorithm used here. Specifically, it seems that each growth unit of a typical stromatoporoid, like each pixel in the model, was largely autonomous in its susceptibility to local conditions; there is little reason to suppose that directions, amounts and patterns of growth were under central control by the organism. However, local autonomy was not absolute; there is no evidence of positive feedback between favourability of position on the structure and growth rate, of the sort that produced the branching simulations of Text-figure 7, so resources gained by favoured parts of the organism seem to have been

distributed. There may even have been a negative feedback mechanism to boost growth at incipient recesses and hence maintain the smoothness of the surface.

The success of this model in producing growth forms which are analogous to real natural structures suggests that it is a useful proxy for interpretation of highly integrated modular organisms such as stromatoporoids. Similarities can also be observed between some of the simulations and other organisms, particularly chaetetids, but also corals, stromatolites and bryozoa. This paper has sought to describe and assess the computer model; forthcoming work will explore its potential for improving understanding of specific specimens and palaeoenvironments. Further experiments with computer models such as that presented here may lead to similar interpretations of organizational level and growth strategies of organisms on the basis of the type of computer algorithm and its parameter values.

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