

# Regulation of astogeny in halysitid tabulates

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The question of whether branching and budding in halysitid tabulate corals was regulated by the availability of nutrients or exposure to waste products is important for taxonomy. Moreover, such regulation could have implications for paleoenvironmental interpretation. Although the statistical and morphological evidence presented here is not unequivocal, it is suggested as a working hypothesis that halysitid astogeny was indeed regulated. This would be in accordance with current theories on the growth of Recent corals and sponges. The simulation results are used to reevaluate functional advantages of the regulation of the halysitid colony.

**Key words:** Halysitidae, Tabulata, astogeny, ecophenotypes, models.

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## Introduction

The Ordovician and Silurian halysitids are usually assigned to the tabulate corals, though it has also been suggested that they were sponges (Kaźmierczak 1989, with reply by Wood *et al.* 1990). The beautiful cateniform colonies of these 'chain corals' can only be fully understood by studying their mechanisms of growth.

The astogeny (pattern formation in colonial organisms) of halysitids has been treated by a number of authors, including Buehler (1955), Hamada (1959), Stasińska (1967, 1980), Lee & Noble (1990), Lee & Elias (1991), and Hubmann (1996). The different types of processes that can occur during astogeny have been identified, but the important question of how, or even if, these processes are regulated according to the changing geometry of the colony has only been mentioned in passing. This problem is addressed below. In particular, the question as to whether astogeny is partly under the control of a diffusive field that surrounds the colony is considered. This field may be set up by the diffusion of nutrients, waste products or specially secreted pheromones.

If such a theory were correct, we would expect the morphology of colonies, especially the sizes of lacunae (closed spaces surrounded by chains) to be affected by environmental parameters such as nutrient availability and water currents. Such eco-phenotypic effects would have consequences both for taxonomy and for the interpretation of paleoenvironments.

## Elements of halysitid astogeny

The growth of halysitid colonies is best studied through serial sectioning. The work of the authors referred to above has clarified many aspects of halysitid astogeny. A new colony was initiated by the settlement of a planula larva on the substrate. This larva formed a protocorallite, that would soon start to bud and produce the first chain. Increase at the end of a chain is termed *lateral increase* ('peripheral increase' has been used by some authors).

Chains may have also branched, either at their ends or internally, initiating new chains (following previous authors, the term 'branching' here applies to chains, not individual corallites). Stasińska (1980) disputed the existence of branching, claiming that apparent branching is nothing but settling of larvae close to an existing chain. Though this may be true in some cases, clear examples of true branching seem to be displayed in specimens studied by Lee & Noble (1990) and Hubmann (1996).

If a chain abutted another chain through lateral increase, it would have made contact and fused with it. In this way, a mesh of chains is produced, closing off open areas (lacunae). Through *interstitial increase*, new corallites could also be initiated between corallites in an existing row, thus elongating it. Neighbouring corallites were then pushed aside through differential growth. Also, some fine-tuning of the geometry seems to have occurred by sideways growth of the corallites, often leading to a polygonalization and regularization of the lacunae. While these processes were taking place, the colony was growing vertically.

The distinction between the *monoplanulate* and *polyplanulate* modes of halysitid astogeny was made relatively recently (Lee & Noble 1990, but see Stasińska 1967 for similar observations). In the monoplanulate mode, a single larva initiated the whole colony. In the polyplanulate mode, several larvae settled, perhaps at different points in time. These larvae initiated their own subcolonies, that later merged into a supercolony. These two modes of astogeny obviously produced somewhat different geometries, at least in the early phases of colony formation.

## Random subdivision?

The simplest null hypothesis is that branching was initiated totally at random, and that lateral increase produced chains that were randomly oriented relative to one another. Apart from the fact that branching without any particular cause is an unsatisfactory explanation, there is evidence that branching in a chain surrounding a lacuna would preferentially occur when the lacuna had reached a certain size (Hubmann 1996). The new chain will then divide the large lacuna into two smaller lacunae, thus maintaining a

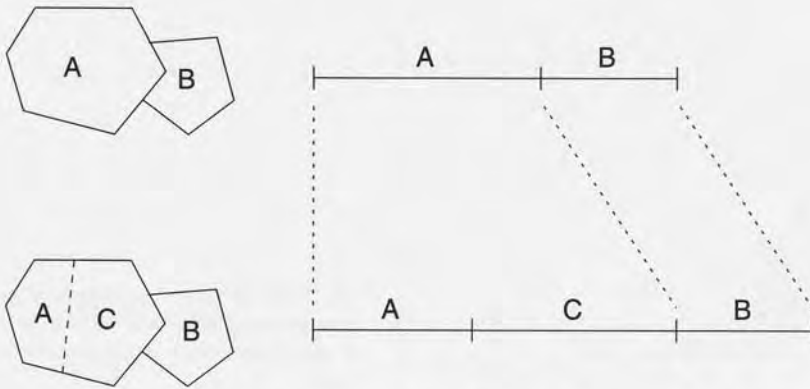


Fig. 1. Colony initially contains two lacunae, termed A and B (top left). Lacuna A then gets divided into two lacunae, termed A and C (bottom left). The perimeters of the lacunae are arranged linearly for theoretical purposes, as shown to the right.

size of lacunae that seems to be characteristic of the species or at least of conspecific colonies from the same location (though lacuna size could also vary during astogeny). A theory will be presented here that suggests a mechanism for such regulated branching.

It is not straightforward to test the null hypothesis of random branching and budding statistically, because there are so many variables and unknown constraints that may have influenced the pattern formation. Nonetheless, some statistical observations are presented here, at least to give an impression of the methodological problems.

For theoretical purposes, it is convenient to imagine the chains surrounding all lacunae as arranged in a line (Fig. 1). If it is supposed that the probability of a branching event is constant and equal for all corallites, and that subdivision divides the lacuna in two daughter lacunae of random proportions, we may view subdivision as a modified Poisson process (meaning that probability of an event is independent of position and earlier events) where points are added to the lines in Fig. 1 with uniform distribution. In an ideal Poisson process, the lengths of the resulting intervals (perimeters of lacunae) will have a negative exponential distribution. In our case however, the length of the new, subdividing chain will have to be added to the perimeter of each daughter lacuna, thus modifying the distribution. Computer simulations show that the hollow-curve appearance of the distribution is not substantially changed by this modification. In Fig. 2 is shown the distribution of sizes of lacunae after 1000 random subdivisions of the unit interval. After each addition of a point on the line, one fourth of the length of the previous interval was added to each subinterval, as would be appropriate for a hypothetical situation where lacunae were continuously kept quadratic and the subdividing chain had a length of one side of the quadrate.

The numbers of corallites were counted around undamaged lacunae in fragments of two colonies of *Catenipora heintzi* (Stasińska, 1967) from the Wenlock of Ringerike, Norway. The distributions of these perimeters, as presented in Fig. 3, are obviously not negatively exponential (Kolmogorov-Smirnov test,  $p < 0.00001$ ), demonstrating that astogeny cannot be explained by totally random subdivision alone. There is a truncation of small sizes and a marked characteristic size. The few lacunae with very long perimeters are extremely elongated, and have relatively small areas.

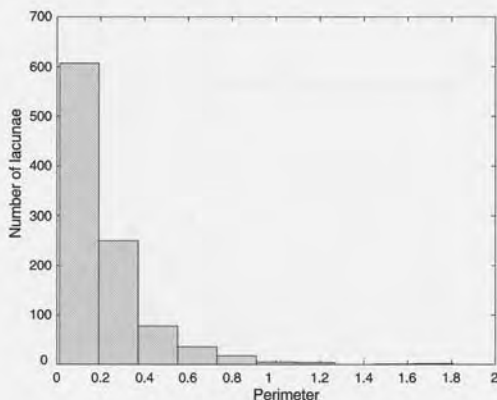


Fig. 2. Distribution of perimeters of quadratic lacunae after 1000 simulated random subdivisions, starting with a single lacuna of one unit length.

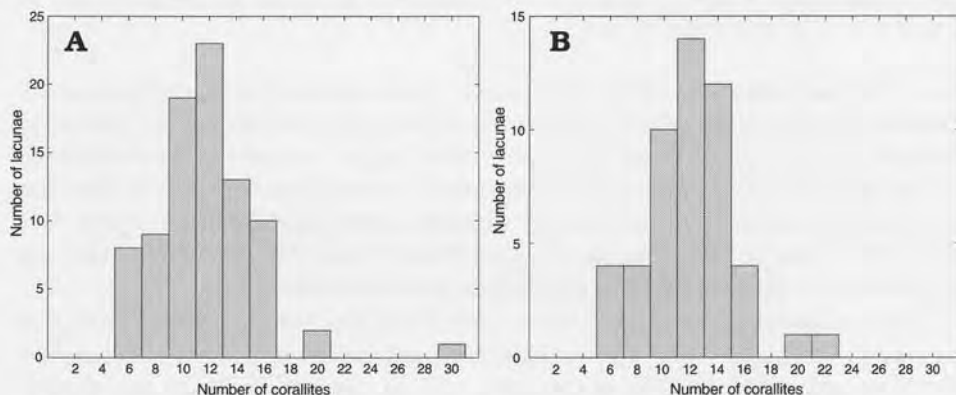


Fig. 3. The distribution of lacuna perimeters, given in number of corallites, in two specimens of *Catenipora heintzi*. Note the truncation of small sizes. **A:**  $N = 85$ ,  $\bar{x} = 12.3$ ,  $\text{var} = 14.1$ . **B:**  $N = 50$ ,  $\bar{x} = 12.5$ ,  $\text{var} = 11.1$ .

Both random branching points and random increase have now been assumed, subdividing the lacunae in a totally arbitrary fashion. While random branching would not be an unnatural assumption, it might be expected that the outshooting chain would diverge at a right angle from the existing chain and then run straight ahead. For very elongated lacunae, this would indeed give almost totally random proportions between the two daughter lacunae, but for more circular lacunae it would tend to divide the lacuna in two daughter lacunae of almost equal size. Fig. 4 shows the result of a computer simulation with 100 divisions of lacunae. The probability of subdivision is proportional to the size of the lacuna (meaning constant probability per corallite), but in contrast with the simulation shown in Fig. 2, where the lacunae were randomly subdivided, the lacunae are now always divided exactly in two. This leads to a distribution which is not negatively exponential, and somewhat more similar to the observed distribution in Fig. 3, with a truncation for small sizes. Note the discrete size classes, which are due to the exactly even divisions of lacunae in the simulation. After addition of some uniform noise to smooth out the notches in the distribution, and scaling to the same mean as in Fig. 3, the null hypothesis of similar distributions has a probability of

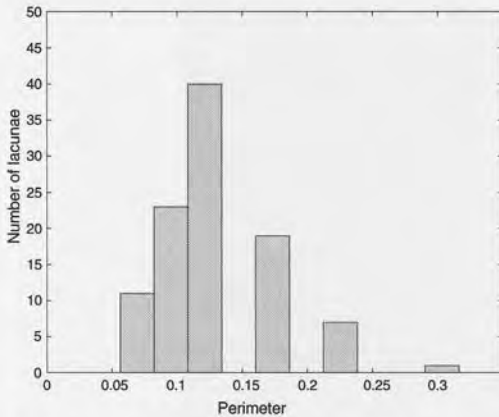


Fig. 4. Distribution of perimeters of lacunae after 100 simulated random subdivisions, starting with a single lacuna of one unit length. Each subdivision leaves two daughter lacunae of equal size.

only  $p < 0.06$  (Kolmogorov-Smirnov), which is admittedly not a very good fit, but this is not surprising given the arbitrarily chosen parameters in the simulation.

From these analyses on the distribution of sizes of lacunae alone, it may thus be difficult to rule out the hypothesis of random branching but equal subdivision. In order to study the problem of branch initiation in isolation, it would be of great interest to test branch positions statistically. This is unfortunately difficult, because branching events have to be observed right at their initiation phase in order to determine their relationship to the surrounding geometry. If a branching position is deduced by looking at a later time horizon, the geometry may have already changed too much to make the observation useful. Also, when the developing chain has made contact at the other end, it is difficult to ascertain the direction of budding, and consequently at which end the chain was initiated. The only way to study a number of branching events in a single colony is to make serial sections with close spacing.

A serial sectioning of a fragment of a colony of *Catenipora heintzi* from the Wenlock of Ringerike, Norway, was performed. Sixty sections were taken at increments of 0.1 mm. In this sample, only seven certain branching events were captured at their initiation. All of these were in lacunae of 'middle to large' size, but no conclusions can be drawn from such a small sample. Further studies of this kind are needed.

## Functional advantages of regulation

Functionally, the morphology of the halysitid colony provided a palisade-like protection against influx of sediment (Lee & Elias 1991). The accumulation of sediment inside the lacunae also helped to stabilize the structure. However, the cateniform morphology and the seemingly regular distribution of lacunae may have had yet another functional aspect. Such a geometry implies a large distance between corallites, under the constraint of continuity of the chains. This would give maximal feeding efficiency (provided that clustering did not give any particular advantage due to cooperation) and maximal distance to other sources of waste products. In simulations of pattern formation involving lateral inhibition, cateniform patterns often occur. For example, such lateral inhibition is an important part of most reaction-diffusion models.



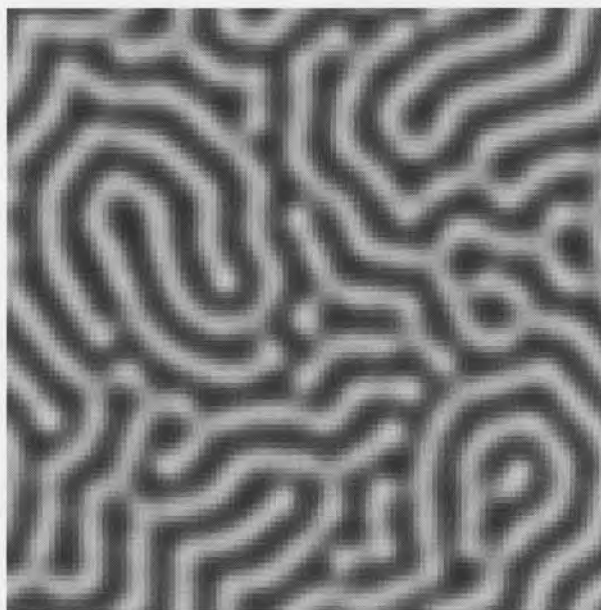


Fig. 5. Emergence of a cateniform pattern using the Gray-Scott reaction-diffusion model.  $F = 0.04$ ,  $k = 0.058$ ,  $D_u = 0.2$ ,  $D_v = 0.05$ . A 100 by 100 grid was used, and run for 2000 time steps.

Fig. 5 shows the result of a particular simulation using the Gray-Scott model (Pearson 1993), which describes a biological or chemical situation where two substances (an activator and an inhibitor) interact in a nonlinear way and such that the inhibitor is produced in and diffuses away from the activated areas.

Maximal feeding efficiency might be accomplished with a hexagonal mesh. Such a geometry is sometimes approximated by halysitids, but more irregular patterns, with some or all lacunae more or less elongated, are more common. If frequency of branching were regulated by the local concentration of nutrients, feeding efficiency would always be maximized under different conditions, at least locally.

## A morphogenetic diffusive field

Kaandorp (1995) was able to simulate the astogeny of modern corals and sponges by assuming that differential growth is regulated by the availability of nutrients. Most of his models calculate the steady-state distribution of diffusing nutrients using the Laplace equation. Insertion of new corallites is then simulated using L-systems (Prusinkiewicz & Lindenmeyer 1990), controlled by the local density of the potential field. Kaandorp (1995) also gives experimental and observational evidence for his models.

A similar model for the formation of cateniform colonies of the halysitid type is proposed here. For simplicity, a two-dimensional model is used, which is most appropriate for relatively flat colonies but may perhaps also be used as an approximation for more hemispherical ones. The corallites are represented by objects having

two-dimensional apical positions. For each time step, these positions are updated, and new corallites introduced, according to certain rewriting rules (in the sense of Prusinkiewicz & Lindenmeyer 1990). According to the classification scheme for morphogenetical models proposed by Prusinkiewicz (1995), this is a *structure-oriented* model (focusing on the development of the components that constitute the structure), with *exogenous control* in the form of a density field set up by the colony. Similar models of branching patterns have been used to explain botanical structures and axon growth (Prusinkiewicz 1995). Cohen (1967) was probably the first to propose a biological model of growth down the gradient of a density field, as suggested below.

The corallites are assumed to have secreted lateral inhibition factors, which could simply be their waste products. An alternative interpretation of the same model, only implying a simple sign reversal in the equations, would be a depletion process where corallites act as sinks in a field of diffusing nutrients (this is the mechanism proposed by Kaandorp 1995). The distribution of the morphogen is computed on a regular grid. Kaandorp computes the steady-state distribution using the Laplace equation, which is somewhat expensive in terms of computation time. Because there is no particular reason to postulate that the distribution has reached the steady state for each time step, we could simply run a few iterations of the diffusion equation instead. Actually, these can be regarded as iterations of a not very effective iterative algorithm for the Laplace equation, and gives similar patterns. However, the steady state is still computed here in order to minimize the number of specified parameters. Also, a decay term is added to the equation, representing removal of waste products (or influx of nutrients). Without such a term, the field inside a closed lacuna could never fall below the minimum value at its boundaries, but would stay almost constant. This follows from the Maximum Principle for the Laplace equation. The time-variant diffusion equation with a decay term is

$$\frac{\partial u}{\partial t} = \nabla^2 u - ku \quad (1)$$

Here, the partial derivative  $\frac{\partial u}{\partial t}$  is the rate of change in the concentration  $u$  over time.

$\nabla^2$  is the Laplace operator, giving in essence the 'curvature' of  $u$  as the sum of the second derivatives in the  $x$  and the  $y$  directions:

$$\nabla^2 u = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}$$

To compute the steady state, we set  $\frac{\partial u}{\partial t} = 0$  and obtain

$$\nabla^2 u - ku = 0 \quad (2)$$

where  $k$  is a constant decay coefficient. Alternatively, the somewhat simpler Poisson equation

$$\nabla^2 u - k = 0 \quad (3)$$

can be used, giving similar patterns. This would model a steady, constant outflux of the signal substance, instead of exponential decay. The concentration is set to zero at the boundary (Dirichlet boundary conditions). For numerical approximation in the computer,

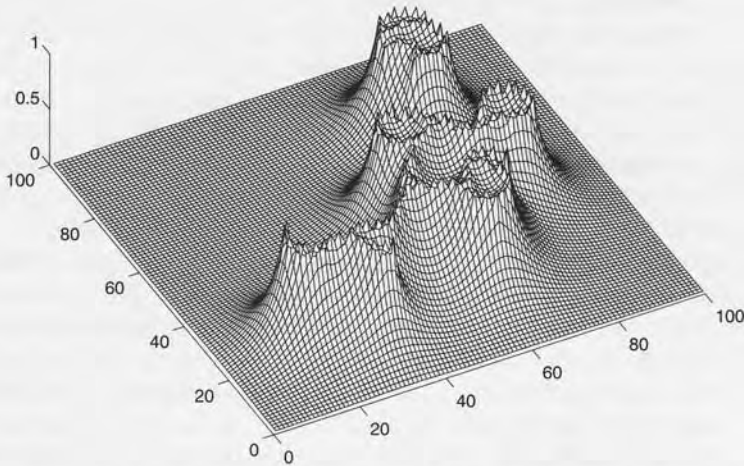


Fig. 6. The diffusive field during a simulation of halysitid growth. Equation (3) was discretized on a 100 by 100 grid and solved with a Gauss solver for banded matrices. Homogenous boundary conditions. Note the depressions inside the lacunae, which would be impossible with the pure Laplace model of Kaandorp 1995.

this continuous differential equation is discretized using a difference method, typically on a grid of 100 by 100 or 200 by 200 nodes. The positions of the corallites are used to set production sources at those locations, modelling the secretion of the signal substance. These sources enter as Dirac-delta terms at the appropriate spatial positions at the right hand side of equation (2). The resulting set of algebraic equations, one for each node in the grid, is solved with a direct Gauss solver for banded matrices (Press *et al.* 1992: pp. 50–54). An iterative method like successive over-relaxation might be more efficient. As a technical side note, a very efficient method might be obtained by taking advantage of the point-formed sources and the fact that the potential field is to be evaluated only at a limited number of positions. For each point  $x$  where the field is to be evaluated, simply take the sum of the Green's functions for the boundary value problem at all corallite positions  $\xi_i$  (Courant & Hilbert 1989: pp. 351–388):

$$u(x) = \sum_i K(x, \xi_i) \quad (4)$$

A typical distribution of the diffusive field using equation (3) is shown in Fig. 6. Since corallites cannot be expected to lie aligned with the grid nodes, some interpolation is necessary. We use simple bilinear interpolation.

## Hypothetical growth rules

Given the types of astogenetic events observed in the fossil material, and the density field proposed in the previous section, a number of hypothetical growth rules to be



included in a computer program can be postulated. A monoplanulate model is used, that can easily be extended to polyplanulate cases (Fig. 10). The rules are as follows:

1. Free ends of chains will continually be elongated through lateral increase. This increase occurs in the direction of the negative gradient of the field, thus giving a tendency for outshooting chains to grow away from other corallites.

2. There is a maximum turning angle, typically set to 22.5 degrees. This is a necessary consequence of the elliptical shape of halysitid corallites. The existence of interstitial tubules, as in *Halysites*, might increase this value.

3. If a chain should collide with another chain, it will make contact.

4. Branching occurs when the strength of the field drops below a certain threshold value, that is, in favorable positions away from other corallites. In the simulations, this threshold value is adjusted to get a 'reasonable' branching frequency in accordance with the fossil material.

5. Existing corallites grow laterally down the gradient, away from other corallites, though this may be modified by rule 6.

6. Neighbouring corallites in a chain cannot be pushed too close together. There is a 'spring' effect that keeps a characteristic distance between neighbours (roughly equal to the mean intercorallite distance).

7. If the distance between neighbouring corallites increases above a certain value due to lateral growth, interstitial increase is initiated. This value would be approximately equal to the maximal intercorallite distance observed in the fossils. The combination of this rule and rule 5 produces a continuous lateral expansion of the colony even if no new chains grow outwards from the periphery.

This set of rules may be contrasted with, for example, the proposed rules for growth in the bryozoan *Stomatopora* given by Gardiner & Taylor (1982), which constitute a 'blind' model (no diffusive field) with branching only at terminal ends. Though most of the rules may appear reasonable, there are at least two basic problems, both in connection with rule 1. The first is that rule 1 gives a 'run-away' effect that causes fast and unlimited lateral increase of the colony. This seems unnatural in view of the fact that most halysitid colonies seem to be laterally constrained. In a somewhat *ad hoc* manner, it is assumed that the colony size is limited by some unknown effect, perhaps connected with the nature of the substrate, which may not be suited for colonization outside a limited area (though small colony size may of course just reflect young age). If we simply assume that lateral increase occurs without regard for the strength of the field, we run into the same problem. An alternative hypothesis would be that lateral increase takes place in the direction of the positive gradient, which would be the exact opposite of rule 1 above. This would stop the escape of chains, and ensure that they turn back and re-establish their contact with the colony. However, this is not in accordance with the radial growth patterns and other observations presented in the next section.

The other problem is that rule 1 makes it difficult for an outshooting chain to make contact with another chain, though such fusion is certainly possible because of rule 2. Again in an *ad hoc* manner, it is proposed that new corallites produce more of the morphogen, or use more nutrients, than older corallites. This makes it possible for a terminal end to approach an old chain, and, at the same time, makes it difficult to turn back against the strong field produced by the new chain itself. In spite of these problems, rule 1 is accepted here because of evidence presented in the next section.

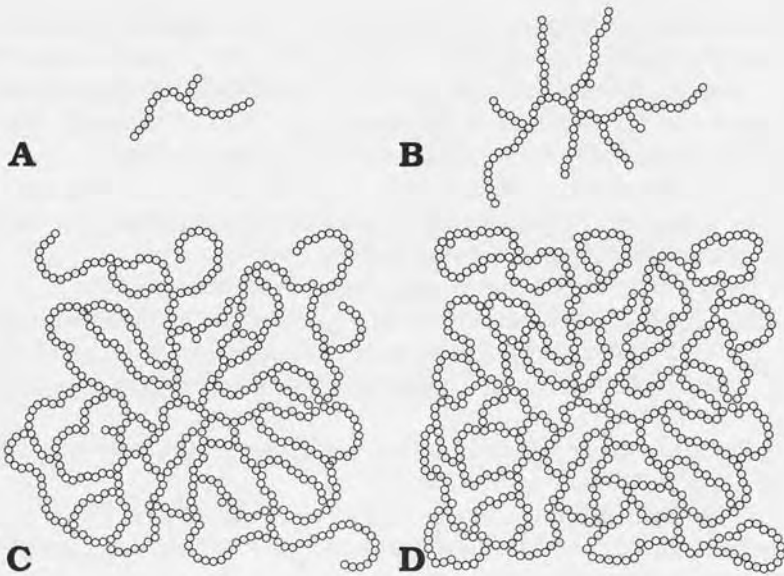


Fig. 7. Computer simulation of halysitid astogeny using the set of rules given in the text. Time steps: 10 (A), 20 (B), 50 (C) and 100 (D).

An alternative idea is that there might be yet another signal, most likely biochemical, that prevents run-away and facilitates a chemotactical 'homing' behaviour towards other chains. Such a 'clustering factor' (Scrutton personal communication) could be balanced against the tendency to grow away from other corallites. While this is certainly a possibility, and further observation on fossil material might substantiate it in the future, it is a somewhat unsatisfactory explanation. First, it is not a parsimonious theory, as it postulates another signal in addition to the signal that produces our diffusive field (whether this field is a simple nutrient distribution field or an explicit pheromonic field). Secondly, the diffusive field of this clustering signal would have a similar geometry to our diffusive field, unless diffusion or decay constants were very different. No additional information would therefore be available to the corallites from the second signal. If there really is a 'clustering factor', it could rather be a response to an especially low concentration of our diffusive factor, causing switching to a chemotactic rather than the normal chemophobic behaviour in order to prevent run-away. This homing mode would have to remain persistent even when concentrations increase again as another chain is approached (in engineering parlance, this could be termed a *hysteresis* effect). This possibility has not been tested by modelling, but seems a plausible alternative to the two *ad hoc* assumptions above.

The causal relationship between lateral growth away from other corallites, producing large distances and tension between neighbouring corallites, and interstitial increase, is guesswork. There is no evidence to rule out the possibility of constant probability of interstitial increase, but some specific trigger for such increase must have existed.

Using these growth rules, a computer program was written. Fig. 7 shows the result of a typical run. To prevent the run-away effect, high field strength had to be imposed at the boundary, simulating unfavorable conditions there. The number of parameters is too large

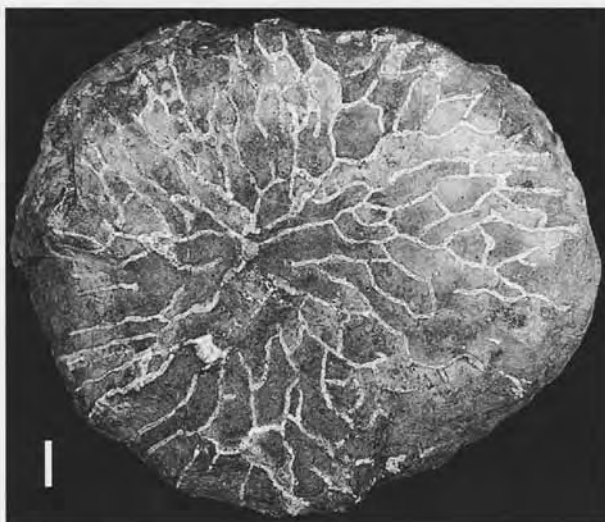


Fig. 8. Base of a corallum of *Catenipora ringerikensis*, PMO 93202. Note the radiating pattern away from the circular shelly fragment. Scale bar 1 cm.

to be presented here, but the complete C program for SGI computers with all parameters included is available from the author. Different values for morphogen production and removal, threshold values for branching, rate of lateral growth and lateral increase, and minimal turning angle, will produce somewhat different patterns. Sizes and shapes of lacunae can be controlled by varying these parameters (Figs 10, 13).

In this model, branching and interstitial increase are controlled by completely different variables. New chains are initiated at low field strengths while interstitial increase is initiated as a response to large distance between corallites in a chain. One might perhaps wish for a simpler theory where these two modes of increase were more closely related, and where branching is nothing but an interstitial increase where one end of the corallite fails to make contact and consequently protrudes from the rank. I have not been able so far to make such a model work, however.

## Evidence for regulation of astogeny

A fundamental question in halysitid astogeny is whether the processes of branching and budding are random, or sensitive to the proximity of other corallites. Some simple observations on fossil material support the hypothesis of a non-random algorithm.

Consider Fig. 8, showing the base of a large colony of *Catenipora ringerikensis* (Stasińska, 1967), Wenlock, Ringerike, Norway. The specimen was taken from the collection of the Paleontological Museum, Oslo (PMO 93202). The impression is that the chains were radiating out from a center where the corallites are attached to a circular shelly fragment. This is interpreted as a situation where the protocorallite(s) has attached to the shelly fragment (a similar attachment of the early corallites to a circular shelly fragment is figured in Buehler 1955: pl. 7: 3). Subsequently, the chains radiated

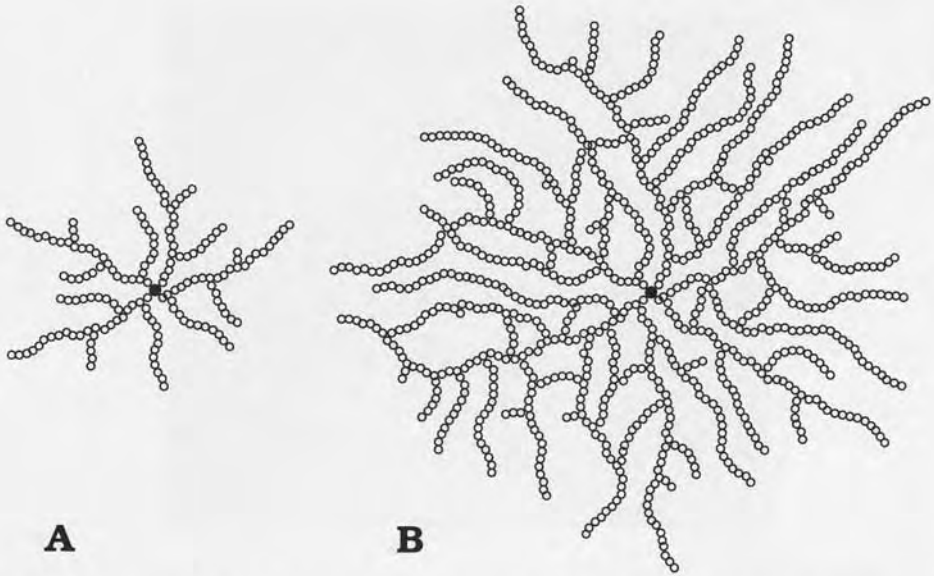


Fig. 9. Computer simulation of halysitid astogeny starting from four protocoallites attached to a 'shell' (black disc). Note the radiating pattern, comparable to the specimen in Fig. 8. Peripheral branches are Y-shaped, while internal branchings are more right-angled. Time steps 20 (A) and 45 (B).

outward, with new chains being produced on the way. These side branches connected to other chains, producing lozenge-shaped lacunae with their long axes oriented radially. This 'escaping' growth pattern is easily explained if it is assumed that the corallites budded and branched in the direction of the negative gradient, growing out into areas where more efficient feeding could be accomplished. Similar radial patterns were observed by Buehler (1955). His pl. 9: 2 and 3, even show a large colony with several centers of radiation. A polyplanulate mode of astogeny can easily explain this arrangement as the fusion of several colonies, each with its independent radiating growth pattern. It should be noted, however, that strict control of length of branches and their angles, without a diffusive field, could produce similar patterns (Gardiner & Taylor 1982).

Branchings in Fig. 8 may be loosely divided into two intergrading groups. One type is Y-shaped, while the other type is more right-angled. It is not necessary to invoke any additional growth rules to explain this bimodality. Branchings close to the periphery of the colony will be low-angled, because the chains are increasing away from the field set up by the whole colony as well as away from the parent chain. These branchings will later become part of the interior of the colony due to lateral expansion. Branchings initiated in the interior of the colony will be more right-angled, because the new chain would escape as fast as possible away from the parent chain, connecting to a parallel chain. Fig. 9 shows a simulation which partly mimics the specimen in Fig. 8. Four protocoallites are attached to a 'shelly fragment', producing a radiating morphology. Y-shaped branchings tend to occur near the periphery of the colony. Y-branches in the interior are ones that were initiated at the periphery at an earlier stage. Right-angled branchings are initiated in the interior, connecting parallel chains.



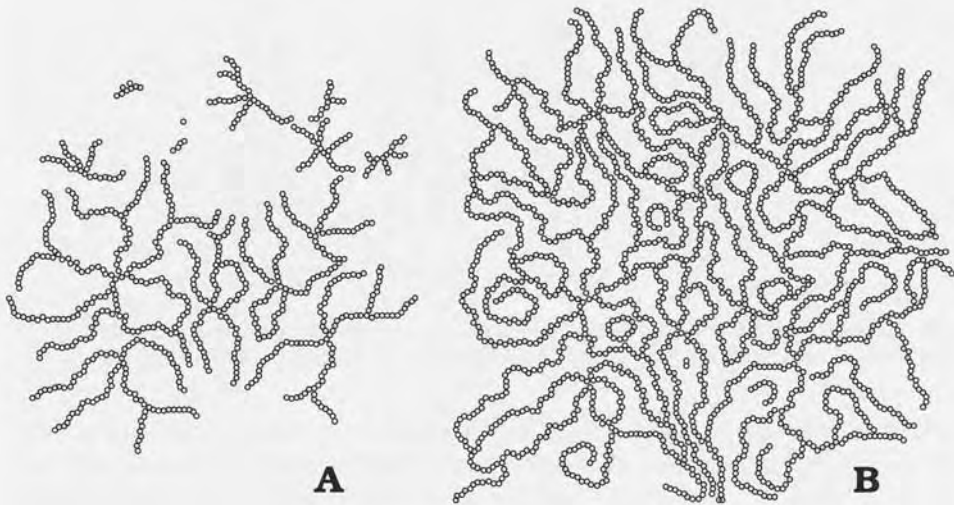


Fig. 10. Computer simulation of halysitid astogeny using a polyplanulate model and maximal avoidance, giving a 'labyrinthine' morphology. Time steps 30 (A) and 52 (B).

'Labyrinthine' halysitids, which grew in highly convoluted patterns of extremely elongated, folded lacunae, maintaining a small but persistent spacing between chains, are of particular interest. There are at least two processes that may have contributed to the formation of such patterns. The first is extreme avoidance during lateral increase, so that new chains find their way between existing ranks, running along 'corridors' until contact with another rank is unavoidable. This would support the hypothesis of lateral increase down the gradient. Fig. 10 shows a simulation using a polyplanulate model, where one new larva settles at a random position in every time step. The assumption of lower morphogen production rate from old corallites has been removed, giving a tendency to avoid existing chains as much as possible without violating the constraint of maximal turning angle. This produces elongated, folded lacunae.

The other way in which a labyrinthine pattern could be produced would be by lateral growth of established corallites away from other chains, keeping a small but persistent distance between ranks, combined with a high rate of interstitial increase which elongates the chains in a limited geometry where folding would be the only way of accommodating them. This would support the hypothesis of lateral growth down the gradient, or, alternatively, the small distance might be maintained through direct contact between the polyps (Scrutton 1997). Buehler (1955) noted cases where labyrinthine patterns seem to have been produced from an early polygonal geometry through excessive interstitial increase and folding of the elongated chains.

Subdivision of very elongate lacunae through branching would not be in good accordance with the diffusive field model, because of the high density of corallites. I have never observed subdivision of very narrow lacunae in Norwegian specimens of *Catenipora heintzi*, but a single odd case was recorded where an obvious interstitial increase led to a situation where the new corallite was slightly offset from its chain



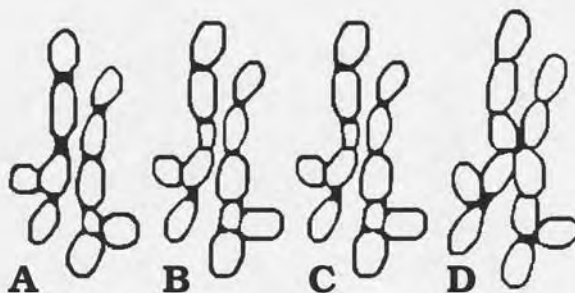


Fig. 11. Serial sections of a specimen of *Catenipora heintzi*, showing interstitial bud that fuses with neighbouring chain. Section levels: 1.4 mm (A), 1.8 mm (B), 2.2 mm (C) and 2.6 mm (D).  $\times 4$ .

(Fig. 11). This caused a collision and fusion with a close parallel chain, thus dividing the lacuna. If anything, this indicates that interstitial increase is not controlled by field strength. Similarly, interstitial increase has been observed at previous branching points, where three corallites meet and density is high.

Lee & Noble (1990) commented that polyplanulate colonies often have an irregular appearance at their bases, presumably as a consequence of the random positions of planula settling. During later astogeny however, the pattern became more ordered and the sizes of lacunae more even. This indicates some regulative ability.

## Ecophenotypic effects

If halysitid astogeny was partially controlled by the distribution of morphogens in the water, it is probable that the morphology of the colony would have been influenced by water currents. This would provide a test for the theory, and also give a useful environmental indicator. Hamada (1959) illustrated a specimen where growth seems to have been strongly biased in one direction, with the protocorallite positioned on one side of the colony (his fig. 6), and he proposed that the growth had taken place against the water currents.

Simulation of water currents should ideally use the full Navier-Stokes equations for three-dimensional hydrodynamics, but this is computationally complicated and expensive. A simplified model assumes only steady, uniform convection in one direction, and is easily incorporated in the program for halysitid astogeny. A steady-state diffusion-convection equation with constant outflux is used (Fletcher 1991: chapter 9):

$$\nabla^2 u - C \frac{\partial u}{\partial x} - k = 0 \quad (5)$$

where  $\nabla^2 u$  is the diffusion term,  $C \frac{\partial u}{\partial x}$  is a term modelling steady transport along the  $x$  axis, and  $k$  is the removal term. This equation is easily generalized to directions of convection other than along the  $x$  axis. In Fig. 12, such a convection term has been added to the program. This convection corresponds to a steady water current from top to bottom in the figures, producing a steeper negative field gradient at the upper edge

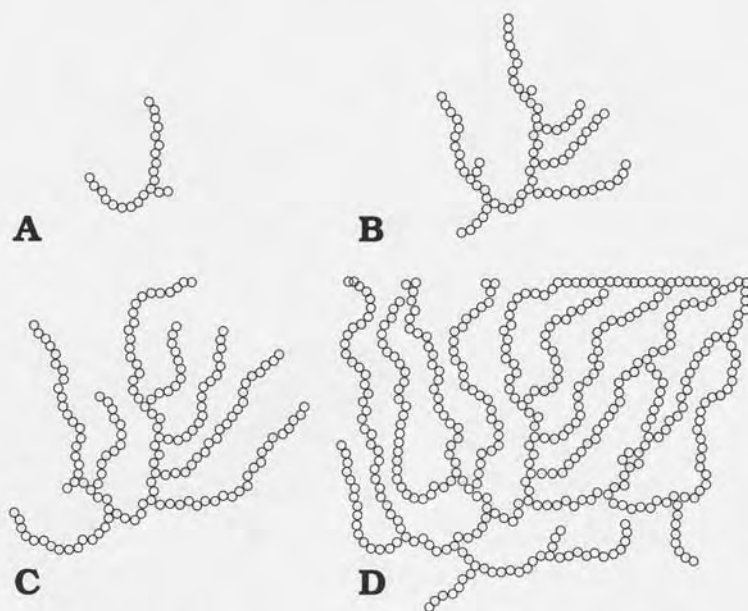


Fig. 12. Computer simulation of halysitid astogeny in a steady water current. Convection corresponds to a water current from top to bottom. Time steps 10 (A), 20 (B), 30 (C), 60 (D).

of the colony. Preferring to grow down the gradient, the corallites show a strong tendency to bud against the current, as theorized for halysitids by Hamada (1959) and as also shown for modern scleractinians and sponges (Kaandorp 1995). The colony gets a drawn-out and 'wind-blown' aspect, compared with the more evenly polygonal and anastomosing character of the simulated colony in Fig. 7.

Another possible ecophenotypic effect would be that increased availability of nutrients would cause higher frequency of branching, giving smaller lacunae. This is demonstrated in the simulation shown in Fig. 13, where the outflux of pheromone (or the influx of nutrients) as given by the parameter  $k$  has been increased compared with the simulation in Fig. 7.

Finally, if halysitids were dependent upon light, they may have shown phototropism that influenced the morphology of the colony (Scrutton 1997). Such effects were modelled by Kaandorp (1995) for scleractinians.

## Conclusion

The study of halysitid astogeny is complicated by several factors, including pre-burial damage, difficulty of extraction from hard matrix, and fast lateral increase. Recovery and serial sectioning of complete colonies are rarely described. Still, halysitids pose intriguing questions of general biological interest, regarding self-organization and regulation in colonial structures. The observations, speculations and simulations given here are of a preliminary nature, but the proposed growth rules should at least be specific enough to be falsifiable and improved upon. More statistical and morphologi-

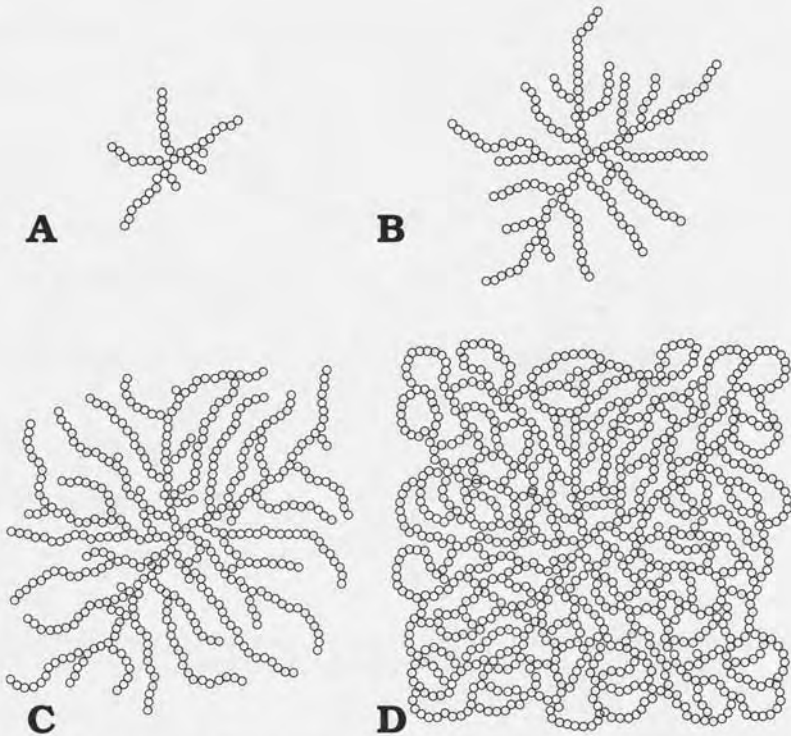


Fig. 13. Computer simulation of halysitid astogeny as in Fig. 7, but with increased rate of removal of pheromone (or influx of nutrients). Characteristic lacuna size then decreases. Time steps 10 (A), 20 (B), 30 (C), 60 (D).

cal studies of complete colonies from different environments, studies of regeneration after damage and of how growth is influenced by competition with other organisms will be necessary to clarify these issues.

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## Kontrola astogenezy u halysitidów

ØYVIND HAMMER

### Streszczenie

Jednym z ważniejszych problemów w badaniach taksonomicznych tabulatów, w tym rozważanych w niniejszej pracy halysitidów, jest stwierdzenie, czy na wzrost ich kolonii (astogenezę), a w szczególności rozgałęzianie i pączkowanie koralitów, miały wpływ czynniki zewnętrzne, takie jak dostępność pokarmu, czy przebywanie w strefie oddziaływania własnych produktów przemiany materii. Potwierdzenie takiego wpływu mogłoby mieć także znaczenie dla interpretacji paleośrodowiskowych. Przedstawione w pracy dane statystyczne i morfologiczne nie zezwalają na jednoznaczne rozstrzygnięcie problemu, jednak sugerują, że astogeneza halysitidów była rzeczywiście kontrolowana przez jakieś czynniki zewnętrzne. Pozostaje to w zgodzie z obecnymi hipotezami na temat wzrostu współczesnych koralii i gąbek. W pracy przedyskutowano również potencjalne korzyści funkcjonalne, jakie dla halysitidów miała kontrola kształtu ich kolonii przez czynniki zewnętrzne.