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Mathematical and Image Analysis of Stromatolite Morphogenesis[1]

M. T. Batchelor,[2] R. V. Burne,[3] B. I. Henry,[4] and S. D. Watt[4]

Stromatolites are internally laminated organosedimentary structures that result from the environmental interactions of Benthic Microbial Communities. They have been traditionally described and classified either by quasi-Linnean taxonomic systems or by morphometric schemes. Neither of these approaches has proved entirely satisfactory. The application of the mathematics of evolving surfaces provides a promising alternative for the modelling and classification of stromatolites in terms of their morphogenesis. The suggestion of Grotzinger and Rothman that stromatolite-growth in general could be attributed to a combination of four processes that constitute the variables of the Kardar–Parisi–Zhang (KPZ) equation has been analyzed and found to be an oversimplification. While some stromatolites can be characterized in this way, because of local growth effects, the majority of stromatolite forms exhibit nonlocal growth characteristic of Laplacian growth. Work is being undertaken to model such growth.

KEY WORDS: stromatolites; morphogenesis; KPZ equation; Laplacian growth.

INTRODUCTION

Stromatolites are internally laminated biosedimentary structures (Logan, Rezak, and Ginsburg, 1964) produced as a consequence of some of the environmental interactions of benthic microbial communities (Burne and Moore, 1987, 1993). Though not organisms themselves, they constituted the only megascopic evidence of life through the Archean and much of the Proterozoic (Awramik, 1991). As Serebryakov (1976) has observed, there have traditionally been two concepts of stromatolite morphogenesis: an ecological concept in which the morphology of stromatolites depends entirely on the conditions of their formation; and a biotic concept, which postulates the existence of some relationship between the morphology of stromatolites and the taxa of microbes to which they owe their formation.

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[2]Department of Theoretical Physics, RSPSE and Centre for Mathematics and its Applications, MSI, Australian National University, Canberra ACT 0200, Australia; e-mail: murrayb@maths.anu.edu.au

[3]Department of Geology, Australian National University, Canberra ACT 0200, Australia.

[4]Department of Applied Mathematics, School of Mathematics, University of New South Wales, Sydney NSW 2052, Australia.

While the role of organisms in determining the form of stromatolite microstructure is still being debated (e.g. Knoll and Semikhatov, 1998; Riding, 1994), there is an increasing body of evidence to suggest that the large-scale form of stromatolites is related in some way to their environmental setting (e.g. Bertrand-Sarfati, 1972; Burne and Moore, 1993 Grotzinger, 1990; Logan, Rezak, and Ginsburg, 1964; Southgate, 1989).

The lack of a suitable scheme for describing and naming stromatolites in a morphogenetically significant way impedes their study. The name was first proposed, as a petrological term, by Kalkowsky (1908) to distinguish these structures from co-occurring oolites in the Buntsandstein of north Germany. Hall (1883) was the first to propose a Linnean binomial for a stromatolite, on the assumption that it was a fossilized organism or colony of organisms (Burne and Moore, 1993). Many workers, especially those with a background in palaeontology, still classify and name stromatolites according to quasi-Linnean systems, such as that proposed by Cloud (1942), despite the fact that stromatolites are no longer regarded as organisms but as biosedimentary accretions. The use of a formal stromatolite classification and nomenclature has been particularly influenced by the pioneering research of V.P. Maslov and his colleagues in the Geological Institute of the USSR Academy of Sciences in Moscow (e.g. Glaessner, 1972; Krylov, 1976; Semikhatov, 1976; Walter, 1972). However, systems of quasi-Linnean stromatolite nomenclature have been neither standardized, generally accepted nor universally adopted.

With the suitability of Linnean nomenclature for stromatolites becoming increasingly questioned (see discussion in Logan, Rezak, and Ginsburg (1964) and references cited therein), Logan, Rezak, and Ginsburg (1964) proposed an alternative approach to the classification of stromatolites based on their geometric form. This limited morphological classification, which recognized only three main growth forms, was too schematic to be of great help (Bertrand-Sarfati and Monty, 1994), and gained only a limited and temporary acceptance (e.g., von der Borch, Bolton, and Warren, 1977). Suggestions for a more rigorous scheme for standardizing the description of stromatolites by improving and standardizing stromatolite morphometry through the use of image analysis and methods of quantitative description have been proposed (e.g. Hofmann, 1976, 1994), but have yet to be extensively adopted.

An illustration of the dilemma which faces stromatolite workers is provided by research on the late Proterozoic Bitter Springs Formation of Central Australia. At Glaessner's suggestion (Glaessner, 1972), Walter (1972) applied principles of taxonomic description and nomenclature, devised in Moscow, in describing and identifying nine distinctive stromatolites from the Bitter Springs Formation. Later, Southgate (1989) undertook a sedimentological facies analysis of the same succession in which he neither utilized Walter's stromatolite taxonomy nor cross referenced his stromatolite descriptions to the forms Walter had described in detail.

Southgate's approach is but one example of a trend among sedimentologists to deal with stromatolites only in the context of sedimentological facies analysis and to provide only cursory and minimal description of the stromatolites themselves (cf. for example, Grotzinger, 1990). By contrast the taxonomic approach of Walter (1972) provides (ideally) a rigorous decription of the stromatolite, but yields little that aids directly in understanding the genesis of the structure. We conclude that a morphogenetic approach would provide a far more powerful tool for analysis and interpretation of stromatolites.

STROMATOLITE MORPHOGENESIS AND RELATED GROWTH PHENOMENA

It is evident that the information contained *within* the stromatolite preserves the history of the evolving surface pattern of the stromatolite, and presents an incomplete record of the interaction of a microbial community and its environment. Properly deciphered, this has the potential to be a powerful means toward the understanding of ancient environments and ecosystems. Two questions are central to the study of stromatolite morphogenesis: how do environmental factors influence the form of evolving surface patterns, and what, if any, aspects of these surface patterns uniquely reflect a biological influence on growth? In this paper we advance this approach through the application of the mathematics of evolving surface patterns to understanding stromatolite morphogenesis and classification.

A potentially fertile approach to understanding stromatolite morphogenesis is to review the literature of growth phenomena to identify examples that produce forms morphologically homologous to those of stromatolites. Little attention has been paid to quantitative analysis of stromatolite morphogenesis until recently.

Hofmann (1994) noted the similarity between the patterns of viscous fingering structures and certain stromatolites. Pattisina, Verrecchia, and Diou (1999) proposed two simulation models of stromatolite morphogenesis. In the first a Diffusion-Limited Aggregation (DLA) Model (Verrecchia, 1996; Witten and Sander, 1983;) with multiple constraints is used to model the evolution of laminar stromatolites over an initially rough surface. The second involves application of various life rules, such as the influence of light on growth, to the evolution of cellular automata.

Grotzinger and Rothman (1996) proposed that stromatolite-growth in general could be attributed to a combination of four mechanisms: fallout of suspended sediment; diffusive smoothing of the settled sediment (that is, sediment moves downhill at a rate proportional to slope) and surface tension effects in chemical precipitation; surface-normal precipitation; and uncorrelated random noise representative of surface heterogeneity and environmental fluctuations. These mechanisms were then fitted to, (or perhaps were derived from), the variables of the

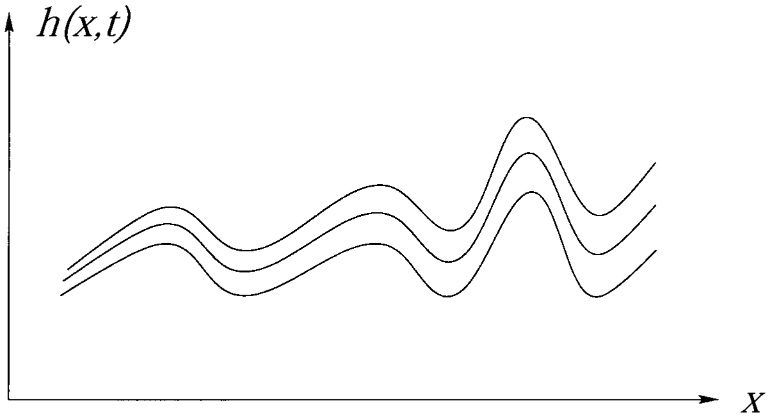

Figure 1. Evolving profile.

Kardar–Parisi–Zhang equation (Kardar, Parisi, and Zhang, 1986): surface tension; surface-normal growth; and white noise.

The Kardar–Parisi–Zhang (KPZ) equation

$$\frac{\partial h(x,t)}{\partial t} = \nu \frac{\partial^2 h(x,t)}{\partial x^2} + \frac{\lambda}{2}\left(\frac{\partial h(x,t)}{\partial x}\right)^2 + \eta(x,t) \quad (1)$$

is the simplest nonlinear stochastic evolution equation for a growing interface. The interface evolves in time above a horizontal baseline, as depicted schematically in Figure 1. The different terms in the KPZ equation represent the competing effects of diffusive surface relaxation, lateral surface growth in a direction normal to the interface, and uncorrelated random noise. The various parameters are

$h(x,t)$—the height of an interface at substrate position x and time t
ν—growth parameter related to surface tension
λ—growth parameter related to lateral growth
$\eta(x,t)$—white noise term

The stochastic KPZ model has been applied to numerous physical growth problems (see, e.g., Barabási and Stanley, 1995), most recently to the growth of stromatolites (Grotzinger and Rothman, 1996). A characteristic property of profiles simulated by the stochastic KPZ equation is that the height $h(x,t)$ of the profile is a self-affine fractal. The fractal property is evidenced by statistical scaling behaviour across several orders of magnitude. However unlike self-similar fractals, different scaling factors are required for different coordinates. The self-affine height profile is described by a surface-roughness–scaling exponent α and a growth-scaling exponent β.

The *roughness* of an interface of extent L can be characterized by the interface width

$$w(L,t) = \sqrt{\frac{1}{L}\sum_{i=1}^{L}[h_i(t) - \bar{h}(t)]^2} \tag{2}$$

where the mean height of the interface is given by

$$\bar{h}(t) = \frac{1}{L}\sum_{i=1}^{L} h_i(t) \tag{3}$$

There are two separate scaling regimes:

$$w(L,t) \sim t^{\beta} \qquad t \ll t_{\mathrm{c}} \tag{4}$$

$$w(L,t) \sim L^{\alpha} \qquad t \gg t_{\mathrm{c}} \tag{5}$$

in which t_{c} is a crossover, or saturation, time, β is the growth exponent, and α is the roughness exponent. The KPZ equation has the exact values $\alpha = 1/2$ and $\beta = 1/3$.

Grotzinger and Rothman (1996) measured the surface roughness exponent of stromatolite growth laminae in peak-shaped stromatolites from the Cowles Lake Formation reef complex and found the same roughness exponent $\alpha \approx 1/2$. Since other growth models (for example the Edwards–Wilkinson model (Edwards and Wilkinson, 1982), which is the same as the KPZ equation but with no lateral growth, i.e., $\lambda = 0$), generate the same roughness exponent this work did not unambiguously validate the KPZ equation for modeling stromatolite growth.

In proposing the KPZ equation as a model for stromatolite growth in general, Grotzinger and Rothman (1996) fail to take into account the fact that surface normal growth would not be expected to be the major accretion strategy of surfaces on which growth is strongly influenced by photoautotrophic behavior, as is thought to be the case for many stromatolites, which would be influenced by shading and the production of branches and overhangs that cannot be characterized by the KPZ equation.

The experimental results of Kahanda and others (1992) are particularly striking in demonstrating both the applicability and limitations of the KPZ model. They examine growing electrochemical deposits on a linear electrode in a quasi-two-dimensional cell, and plot-digitized time-lapsed interface profiles as a function of a variable potential (Figure 2). It should be stressed that these authors emphasize two classes of growth. The first class is what we call Laplacian growth, characterized by nonlocal effects such as screening (see Figure 2(a)). The second are local growth models such as the Eden model, to which the KPZ equation is thought to be applicable (Barabási and Stanley, 1995). The experiments performed examine

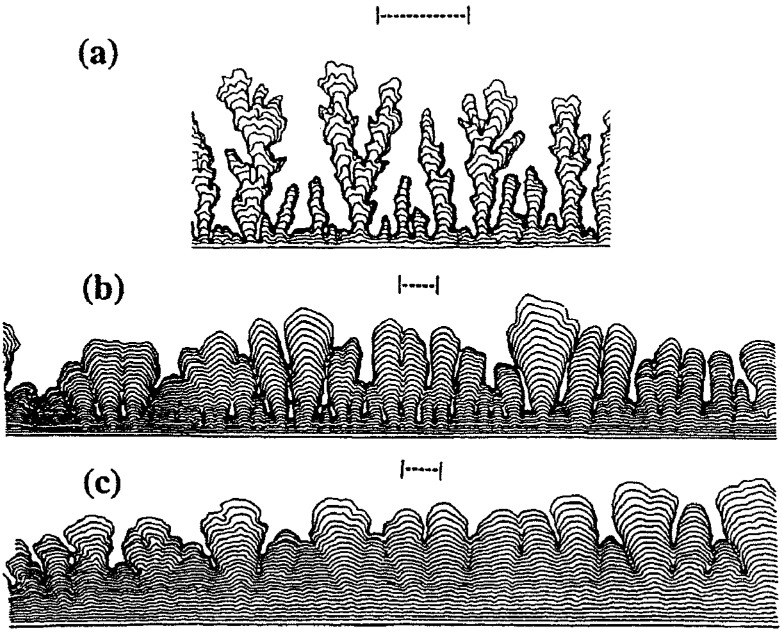

Figure 2. Interfacial profiles of electrochemical deposition. From Kahanda and others (1992). (a) is characteristic of Laplacian growth and (b) and (c) are more characteristic of growth described by the KPZ equation. Scale bar is 0.5 mm.

the competition between such nonlocal and local effects by varying the deposition rate via the current. The analysis performed is on growth obtained in the low current (columnar) regime, as shown in Figure 2(b) and (c). In the columnar regime the surface roughness exponent $\alpha = 0.55 \pm 0.06$ is found from log–log plots of the structure factor. A single-valued height profile $h(x)$ was constructed by taking the highest point for each horizontal position x. Comparison is made with the exact value $\alpha = \frac{1}{2}$ of the KPZ equation. The branched morphology of Figure 2(a), not examined by Kahanda and others (1992), is a classic example of Laplacian growth phenomena.

A further illustration is provided by Sams and others (1997) study of the growth of yeast colonies on a two-dimensional surface. Yeasts are known to be unicellular and characterized by compact colonies. On the other hand, we should recall that some bacterial colonies, with appropriate conditions, provide classic examples of Laplacian-type (dendritic) growth (see figures in Fujikawa and Matsushita, 1989). In their paper, Sams and others present digitized images of the growing colonies. The front of the growing colony is digitized every 5 h. Their resulting contours are shown in Figure 3.

Note the morphological similarity with the electrodeposition experiments in Figures 2(b) and (c).

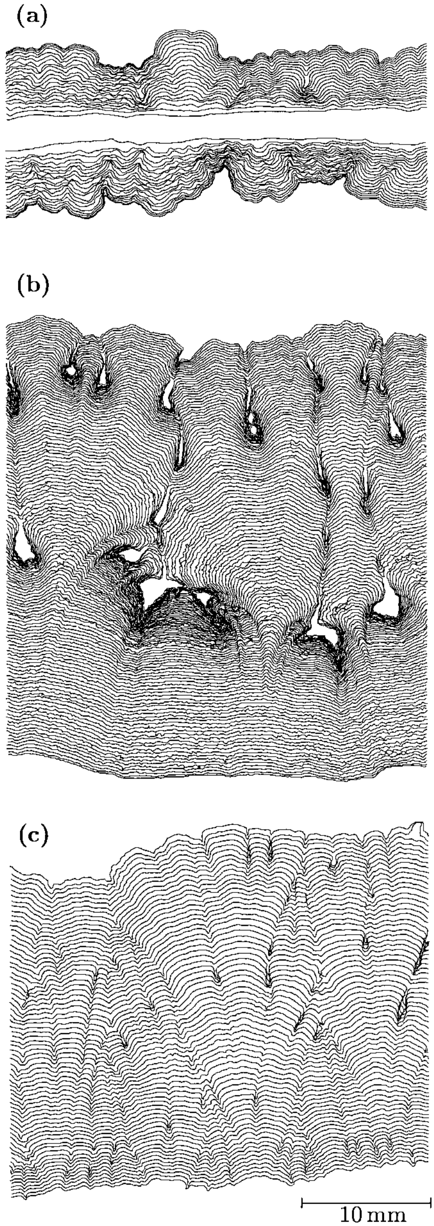

Figure 3. Three examples of growth of *Pichia membranaefaciens* yeast on agarose film. (a) Growth is directed from centre and outwards. (b) and (c) Growth is directed upwards. From Sams and others (1997).

DETERMINISTIC MODEL FOR STROMATOLITE LAMINATION

The limitations of the KPZ equation noted above mean that it cannot be used to characterize many situations thought typical of stromatolite growth. However, one example of stromatolite morphogenesis which may correspond broadly to the mechanisms which Grotzinger and Rothman (1996, p. 423) advance to characterize "stromatolite growth in general," is the occurrence of well-laminated subfossil stromatolites of Marion Lake, South Australia. These are widespread, regularly laminated, fine-grained stromatolites coating the floor of a saline lake (von der Borch, Bolton, and Warren, 1977). Similar stromatolites are forming today in Pink Lake, near Esperence, Western Australia (Burne and Moore, 1987), where they occur as subdued domes in shallow, seasonally exposed locations. Surface-normal accretion of regular egg-shell-like laminae dominates their growth.

We have investigated a deterministic KPZ model for the evolution of the profiles of smooth stromatolite laminae in a sample obtained from Marion Lake and shown in Figure 4. The deterministic limit of the KPZ equation has no noise term.

For perfectly smooth laminae the surface roughness exponent is zero. The evolution of the height profile in the deterministic model is governed by

$$\frac{\partial h(x,t)}{\partial t} = \nu \frac{\partial^2 h(x,t)}{\partial x^2} + \left(\lambda + \frac{\lambda}{2} \left(\frac{\partial h(x,t)}{\partial x} \right)^2 \right) + \upsilon. \tag{6}$$

We recall that the first term on the right models surface relaxation with ν the effective diffusion coefficient and the second term models lateral growth in a direction

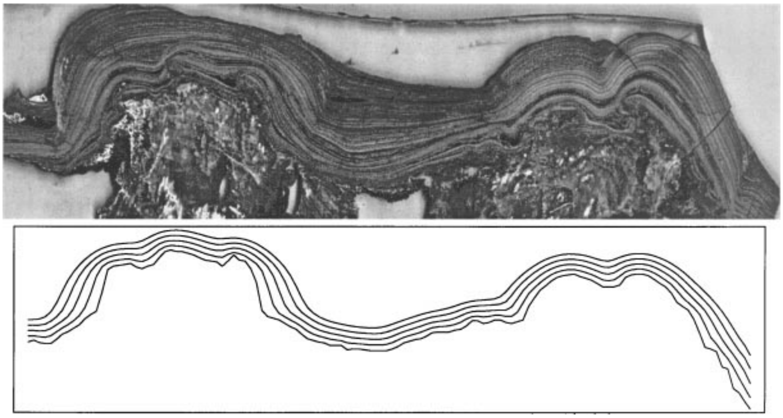

Figure 4. Vertical section of Marion Lake stromatolite laminae (above) and (below) pattern of growth from an an initial profile traced from this specimen. The time snapshots are obtained from the numerical solution of the KPZ equation with $\lambda = \nu = 1$ and $\upsilon = 45.65/185.34$.

locally normal to the interface. Here the third term v represents vertical growth. The constant λ term was omitted from the original KPZ equation, Equation (1), because it had been transformed to a comoving frame. We have not transformed Equation (6) to a comoving frame because we have two constant terms λ and v corresponding to different physical aspects of the growth.

Grotzinger and Rothman (1996) identify the surface normal growth with precipitation and the vertical growth with the fallout of suspended sediment. However, a biotic interpretation may also be possible.

A general solution of the deterministic model can be obtained by employing a Hopf-Cole transformation and then using separation of variables (Kardar, Parisi, and Zhang, 1986). The deterministic model also has the solution (which can be readily confirmed by substitution)

$$h(x, t) = A + (v + \lambda)t - \frac{v}{\lambda}\log(t) - \frac{(x - x_0)^2}{2\lambda t} \tag{7}$$

where A and x_0 are constants. This form of the solution is useful for identifying the asymptotic profile, which is composed of parabolic segments separated by shocks, or sharp discontinuities (in $\partial h/\partial x$) (Kardar, Parisi, and Zhang, 1986).

In order to ascertain the appropriateness of the deterministic model for the Marion Lake stromatolite in Figure 4 we have attempted to extract estimates for model parameters λ and v by fitting parabolic curves to locally parabolic sections of the stromatolite. The points on each segment j are used to find the coefficients a_j, b_j, c_j in the least-squares best-fit parabola

$$h_j(x) = a_j x^2 + b_j x + c_j \tag{8}$$

for that segment. The measurements of a_j, b_j, c_j can then be related to the growth parameters λ and v by comparing (7) with (8). This yields (Batchelor and others, 2000)

$$\frac{1}{a_j} = -\frac{2\lambda}{v + \lambda}(h_j(x_0) - h_0(x_0)) - 2\lambda \tag{9}$$

where

$$h_j(x_0) = c_j - \frac{b_j^2}{4a_j}.$$

Hence from the slope m and intercept b of the straight line of best fit in a plot of $1/a_j$ versus $(h_j(x_0) - h_0(x_0))$ we can deduce values for $\lambda = -b/2$ and $v = -(m/2 - 1)b/2$. In the case of the Marion Lake sample we found $\lambda \approx 185.34$ and

$\upsilon \approx 45.65$. The units for these values of λ and υ are yet to be specified so that the key result here is their ratio, with which we work below. Note too that ν remains a free parameter.

In Figure 4 we show time snapshots of growth obtained from a numerical simulation of the deterministic KPZ equation with parameters $\lambda = \nu = 1$ and $\upsilon = 45.65/185.34 \approx .25$ and for the initial profile taken as a hand tracing from the Marion Lake specimen. The subsequent evolution of the profile in these snapshots is in broad agreement with the smoothing of the subsequent laminae in the stromatolite sample. Larger values of ν result in more smoothing whereas smaller values of ν result is less smoothing (Batchelor and others, 2000).

A similar parameter fit was carried out on the lower portion of a sample of the Early Carboniferous stromatolites of the Ajjers Basin, Algeria (Bertrand-Sarfati, 1994). In this case we obtained the parameters $\lambda \approx 9.42$ and $\upsilon \approx 2.09$. Figure 5 shows (i) a digital scan of the specimen and hand tracings used in the analysis shown as thick white lines; and (ii) time snapshots of growth from a numerical simulation of the deterministic KPZ equation superposed on the hand tracings (grey lines). Again the numerical evolution of the starting profile is in broad agreement with the laminae. The fit is poorest at the edges of the simulation. This is due to the model simulation being carried out on a fixed width domain. It may be possible to improve the agreement by using a wedge shaped domain from a radial version of the KPZ model (Batchelor, Henry, and Watt, 1998). Note too that since the deterministic KPZ model tends to smooth out interfaces it cannot provide a model for the upper portion of the Carboniferous stromatolite which is becoming increasingly dendritic (suggestive of Laplacian growth).

The analysis of the Marion Lake and Algerian samples leads us to suggest that in the case of rough as opposed to smooth stromatolite laminae the stromatolite might be classified according to the roughness exponent α and the growth exponent β. However if the laminae are smooth then a more appropriate classification scheme would be in terms of the growth parameters, ν, λ, υ. In this work we have shown how to estimate two of these parameters, λ and υ from field measurements based on a deterministic KPZ model.

CONCLUSIONS

This analysis has shown that the mathematics of evolving surfaces can be usefully applied both to model stromatolite morphogenesis, and to classify stromatolite forms in an environmentally significant way.

The KPZ equation can be used to simulate the growth patterns of stromatolites, such as the Marion Lake examples, in which surface-normal growth dominates. However, Grotzinger and Rothman's proposal (Grotzinger and Rothman, 1996)

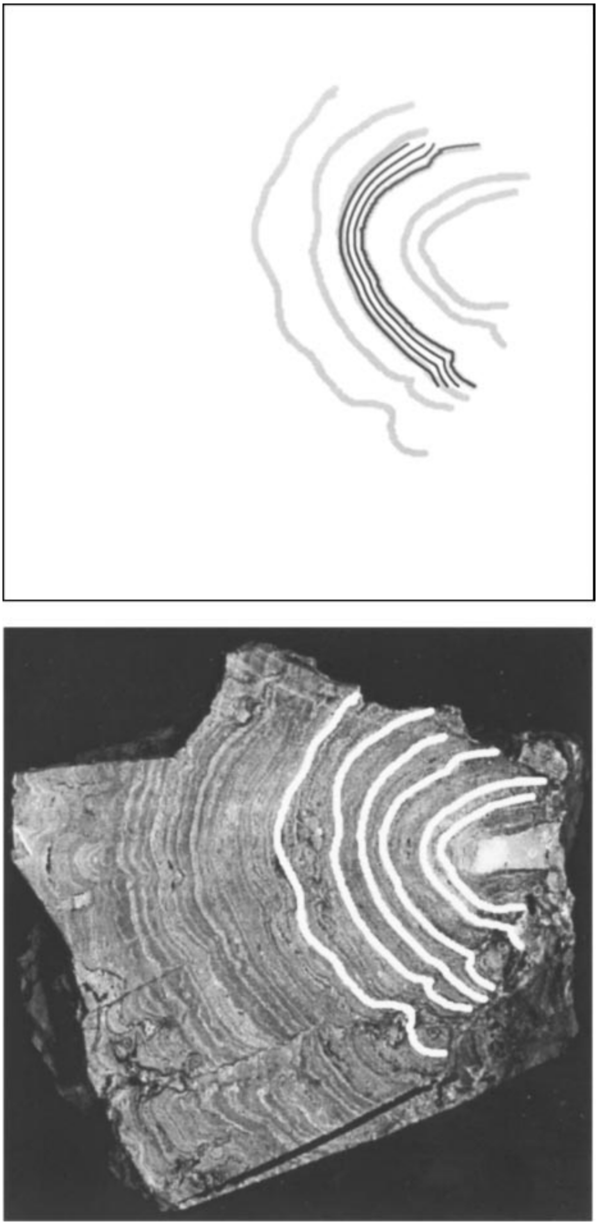

Figure 5. Vertical section of Ajjers Basin stromatolite laminae showing hand tracings (thick lines) and results from a numerical simulation (thin black lines) of the KPZ equation with $\lambda = \nu = 1$ and $v = 2.09/9.42$.

that stromatolite-growth *in general* could be represented by the KPZ equation has been shown to be untenable, since the majority of stromatolites are characterized by branching, sheltering and other complex forms that characterize nonlocal Laplacian growth, rather than local Eden growth. We are currently investigating the application of other mathematical approaches to understanding the morphogenesis of a range of representative stromatolite samples for which the KPZ equation does not apply.

For example, an insight to the evolution of complex stromatolite forms (Krylov, 1976) is provided by the modeling of snowflakes (Batchelor and Henry, 1996; Fig. 5) in which the variation of parameters during growth produces a sudden branching of the growth-structures. Interesting examples of similar effects in complex stromatolite morphogenesis are provided by the spontaneous branching that occurs at a specific horizon in the growth of some domical stromatolites. Figure 6 illustrates an example described by Walter (1972) from the Bitter Springs Formation that exhibits this growth pattern. Southgate (1989) has argued that this

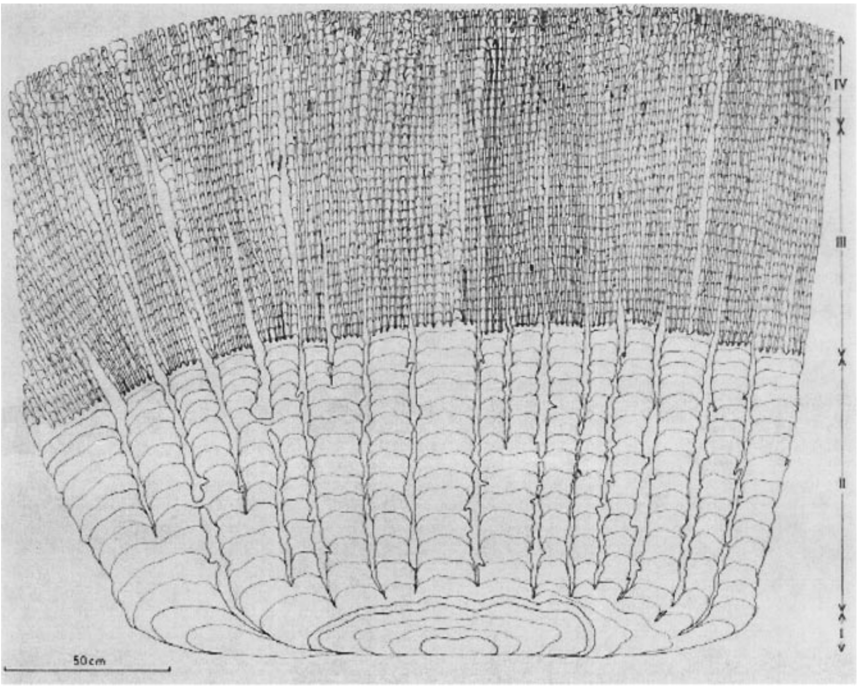

Figure 6. Inzeria initia, one of several of the branching stromatolite forms described by Walter (1972) from the Bitter Springs Formation, Amadeus Basin, Northern Territory, Australia. Note the tendency for simultaneous branching of the structure at successive levels. Reproduced from Text-Fig. 40 of Walter (1972).

branching might be explained by changing water depth, but it might equally be due to a change in one of several other environmental variables.

An indication of the morphological effects of altering variables of surface growth that might be anticipated from this approach is given by analagous results obtained from modeling triangular lattice growth (Batchelor and Henry, 1996; Fig. 3) and square lattice growth (Batchelor and Henry, 1996; Fig. 4) by surface tension modified Darcy's law with surface relaxation, or by the "communication walkers" model of Cohen, Czirok, and Ben-Jacob (1996).

The challenge is now to both examine the suitability of these various mathematical models to the understanding of the evolution of stromatolite forms and to identify the specific environmental parameters responsible for such variation.

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NOTE ADDED

After finishing this work we became aware of two further papers in which the analogy between stromatolite morphology and growth governed by the KPZ equation and diffusion-limited aggregation is discussed (Grotzinger and Knoll, 1999; Pope and Grotzinger, 2000). Another striking example of laminated KPZ-type growth is seen in the paper-burning experiments of Myllys and others (2000).

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