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Translation of energy into morphology: Simulation of stromatolite morphospace using a stochastic model

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Abstract

Stromatolites are examples of an iterative system involving radiate accretive growth of microbial mats, biofilm and/or minerals that result from interaction between intrinsic and extrinsic factors, which progressively shape the final morphology. These interactions can neither be easily described by simple mathematical equations, nor by simple physical laws or chemical reactions. Therefore, a holistic approach that will reduce the system to a set of variables (which are combinations of natural variables) is proposed in order to create virtual morphologies which will be compared with their natural counterparts. The combination of both Diffusion Limited Aggregation (DLA) and cellular automata (CA) allows the exploration of the stromatolite morphological space and a representation of the intrinsic and extrinsic factors responsible for natural stromatolite morphogenesis. The holistic approach provides a translation in simple parameters of (1) the way that energy, nutrients and sedimentary particles reach the active surface of a future build-up, (2) how these elements are distributed and used in order to create morphology, and (3) how simple environmental parameters, such as sedimentation, can disturb morphogenesis. In addition, most Precambrian stromatolite morphologies that are impossible to produce with numerical modeling such as the Kardar–Parisi–Zhang (KPZ) equation can be simulated with the DLA–CA model and this, with a minimum set of variables.

Keywords: Diffusion Limited Aggregation (DLA); Cellular automata (CA); Stochastic model; Stromatolite morphospace; Intrinsic and extrinsic parameters

1. Introduction

Stromatolites have dominated the fossil record for over 80% of the Earth's history (Walter, 1994; Grotzinger and Knoll, 1999) making them the most resilient ecosystem on Earth. These organo-sedimentary structures are situated at the interface between the biosphere and the lithosphere. The interaction between biological and geological activities resulting in stromatolite formation has had a profound influence on the evolution and function of life on this planet, playing a major role in regulating global cycles of major elements and sedimentation (e.g., Kasting, 1991; Holland, 1994, Hoehler et al., 2001). However, the term 'stromatolite' has had many different definitions since it was first introduced by Kalkowsky in 1908 (see discussion in Riding, 2000) and some doubts persist regarding the biological origin of some Precambrian forms. Stromatolites are interpreted as laminated microbially-induced sedimentary structures that refer to genetic features in the definition (Kalkowsky, 1908; Riding, 1991, 2000), whereas authors favor a descriptive definition that emphasizes lamination and morphology (Semikhatov et al., 1979, see also Grotzinger and Knoll, 1999). According to the latter definition, any structures showing a laminated

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morphology initiated from a point or a limited surface could be called stromatolites. However, the growth of Recent stromatolites are microbially-mediated or at least include a strong organic component (e.g., Golubic, 1976; Riding, 1991, 2000; Reid et al., 2000; Seong-Joo et al., 2000). Burne and Moore (1987) introduced the term 'microbialite' as organosedimentary deposits of benthic microbial communities and, following this definition, stromatolite can be seen as a type of microbialite showing lamination as a specific feature. Unfortunately, only a few fossil forms contain remains of the microorganisms that are supposedly responsible for their formation (Grotzinger and Knoll, 1999). Therefore, specialists have mainly based stromatolite classification on morphology and laminae patterns. The Russian school initiated by Maslow even proposes the Linnean binomial classification of Precambrian stromatolites for biostratigraphical purposes (e.g., Semikhatov, 1976). This classification is still in use for stromatolites that were thought to represent organisms (e.g., Burne and Moore, 1993). On the other hand, a highly detailed morphological classification was established by Hofman (1994).

This paper proposes an approach to understanding stromatolite morphogenesis through numerical simulation. A stromatolite can be compared with a 'biogeochemical engine' that translates energy into morphology. The top active surface of the deposit is situated at the water-sediment interface, where all exchanges take place (Jorgensen and Des Marais, 1990). In other words, the boundary is the place, where energy and nutrient fluxes are translated into morphologies through iterative processes. Most stromatolites are formed in environments where bacteria and organic molecules are present and can be actively or passively included in the build-up. The microbial ecosystem at the top of stromatolite plays the role of a filter that enhances, inhibits, or passively witnesses the growth process, according to whether microbial composition and metabolic activity can or cannot influence carbonate precipitation or sediment trapping and binding. Thus, emergence of stromatolites results from interactions and balance between intrinsic (microbial mat or biofilm) and extrinsic factors (environmental conditions) that are responsible for the explosion of the morphological space in the fossil record. This study investigates this morphological space using a DLA–CA (Diffusion Limited Aggregation–Cellular Automata) model. This model simulates stromatolite emergence through interaction of a set of holistic variables, which are themselves a combination of 'natural' variables of the system. These holistic variables will translate the behavior of energy, nutrients, and particles from the water column to the top of the stromatolite as well as the distribution of these components within the active surface (a process called relaxation; Barabasi and Stanley, 1995). In addition, intrinsic factors will be simulated through cellular automata (CA), in which simple transition rules will control the local growth. Comparisons will be made with natural stromatolite morphologies. In particular, branching and columnar forms will be tested since such morphologies are common in fossil stromatolites and are difficult to produce with other numerical models such as the Kardar–Parisi–Zhang (KPZ) equation (Verrecchia et al., 2004).

2. Background

Modern stromatolites are perfect examples of an iterative system involving radiate accretive growth (Kaandorp, 1994, 1995) of microbial mats, biofilm and/or inorganic minerals. This growth results from interaction between intrinsic and extrinsic factors (e.g., Reid et al., 2003a), progressively shaping the final morphology (Fig. 1). Keeping in mind that doubts persist about the microbial or organic origin of certain Paleozoic forms (Grotzinger and Knoll, 1999), 'confirmed biogenic stromatolites' are generally considered as stacked microbial mats or biofilms, which are able to bind sediment and precipitate calcium carbonate. The stacking pattern responsible for the final morphology thus records a combination of environmental parameters and inherited microbiological factors.

2.1. Intrinsic factors—the microbial mat

The microbial mat at the origin of most stromatolite formation can be seen as a 'light-driven engine' (Fig. 1), where cyanobacteria furnish the primary bulk of the organic matter, which is recycled by diverse bacteria. The photoautotrophic cyanobacteria are able to reduce CO_2 into organic compounds, which are degraded through aerobic and anaerobic respiration. In nutrient-limited environments (N-limited for example), microbial mats are able to sustain life through efficient metabolite (element) recycling (Krumbein, 1983; Van Gemerden, 1993). In most microbial mat ecosystems, light is the dominant component that drives the system, except for other essential nutrients needed for biosynthesis. However, a microbial mat is not a stromatolite. Stromatolites are stacked microbial mats, which were able to lithify and/or 'trap and bind' grains in order to

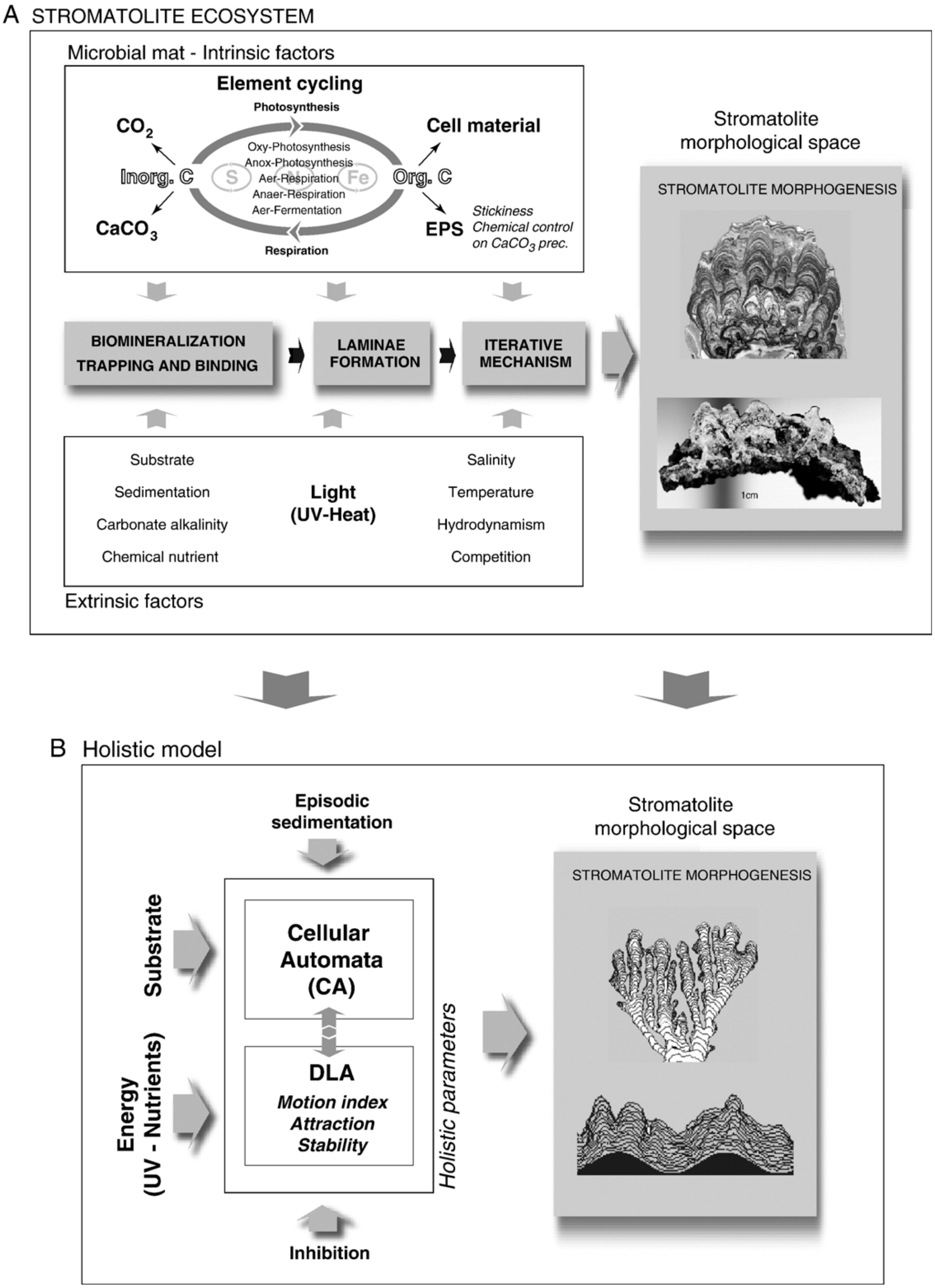

Fig. 1. The stromatolite ecosystem and its holistic translation. (A) Interactions between intrinsic (microbial mat) and extrinsic (environment) factors lead to stromatolite morphogenesis in the natural stromatolite ecosystem. The complexity of the stromatolite growth can be assessed at the microscale (biomineralization, ‘trapping and binding’), mesoscale (laminae formation) and macroscale (iterative mechanism leading to morphology). (B) The holistic approach reduces the stromatolite ecosystem to a set of variables (which are a combination of natural variables) that allows the translation of the intrinsic (via cellular automata) and extrinsic (via DLA model) factors. This translation of energy into morphology allows a thorough investigation of the stromatolite morphospace.

create new substrates in time. Trapping and binding of sediments are performed through production by bacteria of extracellular polymeric secretion (EPS) enhancing the 'stickiness' of the mat (e.g., Reid et al., 2000). Numerous processes lead to carbonate precipitation in microbial mats (e.g., Berner, 1971; Krumbein, 1974; Ehrlich, 1996; Schultze-Lam et al., 1996; Dupraz and Visscher, 2005). Uptake of CO_2 through oxygenic photosynthesis inducing a local increase in alkalinity can be a source of carbonate precipitation (Pentecost and Riding, 1986; Pentecost and Bauld, 1988; Merz, 1992; Verrecchia et al., 1995; Thompson et al., 1997). However, the environment may have low dissolved inorganic carbon and a high Ca^{2+} concentration in the medium for cyanobacteria to precipitate carbonate in their sheaths (Arp et al., 2001; Merz-Preiss and Riding, 1999). In modern marine environments, this mechanism is generally not directly responsible for stromatolite lithification. Other bacteria, mainly sulfate-reducers, associated with degradation of EPS, induce the precipitation of $CaCO_3$ (e.g., Reid et al., 2000; Visscher et al., 2000; Dupraz et al., 2004, Dupraz and Visscher, 2005).

The mechanism leading to biofilm lithification has an impact on the microstructure and the morphology of the precipitated lamina (one layer of lithified microbial mat). The composition of the microbial mat and the way in which microbial communities obtain their energy can thus affect global stromatolite morphogenesis. For example, the roughness of the mat is sometimes translated from the bacterial composition of the mat (e.g., Grotzinger and Knoll, 1999). Entophysalidaceae (Cyanobacteria) are known to build rougher laminae in Shark Bay stromatolites than *Schizothrix* (e.g., Reid et al., 2003b). However, mats that show strong surface roughness are not necessarily translated by rough lithified carbonate layers. The micromorphology of these layers is also conditional upon the location and the nature of the lithification (in the sheath of the cyanobacteria, EPS-mineralization, or trapped grains).

Genetic predisposition of certain cyanobacteria can also create specific morphologies. For instance, *Scytonema* sp. can arrange their filaments to create pustular or cup-shaped forms, which can develop knobby or massive morphologies (Mann and Nelson, 1989). Recent forms described in hot springs also develop peculiar arrangements of filaments called 'conoform' stromatolites, often presented as an equivalent for the Precambrian stromatolites *Conophyton* (Walter et al., 1976). This control on build-up morphology is clearly related to intrinsic parameters.

2.2. *Extrinsic factors—environmental parameters*

Light and sedimentation are key elements of stromatolite ecosystems. Light will fuel the 'light-driven' microbial mat responsible for the local stromatolite growth. The equilibrium between sedimentation and mat growth (and degradation) mainly controls stromatolite development, especially those built through trapping and binding of sediments associated with $CaCO_3$ precipitation (Grotzinger and Knoll, 1999). These stromatolites result from a combination of upward growth of microbial mats and periods of sediment deposition. Thus, equilibrium between biological production/motility and sedimentation must be found in order to avoid dramatic sediment accumulation (burial) or sediment starvation (lack of vertical growth). Episodic increase in sedimentation input can initiate branching formation through preferential accumulation in the microdepressions of the mat; therefore growth of topographic highs is privileged.

Other extrinsic factors have a strong impact on stromatolite morphology, i.e., salinity, nutrient supply, current velocity, sediment grain size distribution, and calcium carbonate saturation. Distribution of chemical agents and nutrients in the water column plays a major role in the development of stromatolites. Ion and nutrient transport in the water column are subject to hydrodynamic energy. In turbulent water of an open system, nutrients are brought into the system in sufficient amounts. Coral reefs are good examples of such organisms preferentially thriving in agitated and well-oxygenated environments. However, changes in hydrodynamic regimes result, among other things, in a modification of the nutrient and ion distribution in the water column (flow regime or diffusion regime). The effect of nutrient diffusion and flow is well known to influence coral morphologies (Kaandorp et al., 1996). Low ion and nutrient concentrations in the water column can produce similar effects on stromatolite morphology. Thin, columnar, and branching forms develop in less turbulent protected environments, whereas massive and planar forms are produced in deeper and more agitated environments (Grotzinger, 1989; Kah and Knoll, 1996; Bartley et al., 2000).

3. Modeling approach

3.1. *How to build a numerical model of the stromatolite ecosystem*

As discussed above, stromatolite growth results from the interaction of intrinsic (microbial ecosystem) and extrinsic (environmental) parameters (Fig. 1). Both sets of parameters control the iterative mechanism at the origin of the final morphology at different scales. Unfortunately, these interactions can neither be easily described by simple mathematical equations, nor by simple physical laws or chemical reactions. In addition, the exhaustive nature and the suitability of environmental parameters used for a growth model can be of doubtful validity. Therefore, approaches other than a detailed translation of each component of the stromatolite system into a complex integrative model have to be investigated in order to create virtual morphologies that will be compared to their natural counterpart. A holistic approach (Fig. 1) will reduce the system to a set of variables, which are combinations of natural variables. Some of these variables will be easily attached to natural parameters, such as sedimentation. Others will be set as a complex combination of parameters in which only the final product will be taken into consideration.

3.2. Numerical models—KPZ equation

The non-linear equation of Kardar–Parisi–Zhang (KPZ equation; Kardar et al., 1986) simulating profile evolution of a growing interface is used for modelization of various growth problems (Barabasi and Stanley, 1995). A modified version of the KPZ equation has been proposed by Grotzinger and Rothman (1996) in order to question the biogenic origin of some stromatolites (Grotzinger and Knoll, 1999; Batchelor et al., 2004). More recently, extensive investigation of this equation as a model for biotic stromatolite growth was made by Batchelor et al. (2000, 2004, 2005), which notably validated a biotic origin for the controversial coniform stromatolites *Conophyton* through simulation.

The KPZ equation includes parameters such as surface-normal accretion, surface tension, and noise that allow insight into morphogenesis of simpler stromatolite forms (Batchelor et al., 2004). This non-linear deterministic model produces iterative vertical growth of regular, smooth and compact laminae. However, this model can be unstable under certain conditions (Pattisina and Verrecchia, 2002; Pattisina, 2003) and can only simulate the growth of massive stromatolites (flat, domal, or coniform). Lateral growth limitation does not allow production of branching forms of stromatolites that are often observed in the Proterozoic (Batchelor et al., 2000; Pattisina, 2003).

3.3. New model DLA–CA

The model used to investigate stromatolite morphological space is based on the ‘Diffusion Limited Aggregation’ (DLA, Witten and Sander, 1981, 1983) model combined with Cellular Automata (CA; e.g., Wolfram, 2002). The model is written in C++ and is available by writing to the corresponding author.

Diffusion limited aggregation (DLA) is the formation of aggregates of particles undergoing Brownian motion (random walk) until contact is made with a cluster (aggregate) or a substrate. Particle movement can be seen as a diffusion process, which is different from a normal flow system where all particles move in approximately the same direction. The shape of the cluster is controlled by the ability of particles to reach the cluster. In environments with low particle concentration, the aggregation is performed one particle at a time and can be very slow. Surface roughness progressively increases with high points of the cluster ‘catching’ more particles to the detriment of the inner region or ‘cryptic’ region of the cluster. Thus, not all parts of the build-up (cluster) have equal growth probabilities. Recently, this type of aggregation was used to model the growth of viscous fingering phenomena in hydrodynamics (Bogoyavlenskiy, 2001) and the growth of tumors (Gazit et al., 1997), dendrites and snow-flakes (Nittmann and Stanley, 1986, 1987), and bacteria (Matsushita and Fujikawa, 1990). Use of the DLA model also introduces the notion of self-similarity, which releases the model from scale restraints (fractal aspect of produced images). Different phenomenon can thus be modeled at various scales with the same tool.

The use of the DLA model to generate stromatolite morphology was first introduced by Verrecchia (1996). Attempts were also proposed by Chan and Grotzinger in a review of fossil stromatolites (in Grotzinger and Knoll, 1999). In the DLA–CA model, the DLA part simulates the main extrinsic growth factors of stromatolites because it represents the external flux of matter leading to build-up growth. The originality of the present paper is the association of the DLA growth model with a simple cellular automata (CA) engine. Cellular automata are systems of cells showing simple local interactions that are able to describe complex global behaviors (Wolfram, 1983, 1984). In this system, time and space are discrete variables, i.e., the space is subdivided into cells considered as individual entities that have a defined state at a time t. The evolution from one state (time t) to another ($t+1$) is described by transition rules and the state of the cell at the time t. The growth related to cellular automata is called 'local', because this growth does not depend on the global structure of the build-up, but on simple transition rules, locally determined as a function of the state of one cell and its neighbors. The combination of both DLA and CA approaches allows a better exploration of the stromatolite morphological space and a better representation of the intrinsic and extrinsic factors responsible for natural stromatolite morphogenesis. In addition, the model proposes a set of holistic parameters allowing a better tuning of DLA growth.

3.4. Parameters of the model

3.4.1. Attraction and stability distance

The DLA model generates more than one particle at a time for the simulation ('Mutiparticle Biased Diffusion Limited Aggregation' — MBDLA; Sánchez et al., 1994). The particles follow Brownian motion before reaching the active surface (the top layer of the build-up) of the stromatolites (Fig. 2A). The *attraction zone* is defined as the region above the active surface, where the particles are attracted to the substrate following a straight line perpendicular to the substrate (exiting the Brownian motion). The attraction zone boundary is built by the vectors that define the *attraction distance* (Fig. 2B1). The attraction distance is a representation of the attraction force of the build-up and can be modified from one simulation to another. The roughness of the active surface and the size of the attraction zone can generate '*protection zones*', where no particles are available for the active surface and therefore no growth is possible (Fig. 2B1). Increasing the *attraction distance* leads to larger protection zones that will produce the formation of wider-spaced columnar or branching morphologies (Fig. 2B2). The reduction of the *attraction distance* decreases the protection zone that will result in massive morphologies (Fig. 2B3).

The *stability distance* refers to the relaxation capacity of particles after the contact with the active surface. In the DLA model of Witten and Sander (1981), particles directly stick to the aggregate at the point of contact and no further movement is applied to particles. This process results in the formation of dendrites. The DLA–CA model proposed in this study involves a relaxation, i.e., the particle will move to a more stable position using less energy. The *distance of stability* represents a radius in which the particle can move on the active surface to find a more stable area (Fig. 2A). The most stable position is the position where the attraction force of the aggregate on the particle is the strongest, i.e., the position having maximum contact with the aggregate (maximum of stability weight, Fig. 2A). Because gravity directly affects the distance of stability, the position compared to the altitude (the lowest position) will decide between two points that have the same stability weight.

By varying both attraction and stability distance, it is possible to cover most of the morphological space of massive and branching stromatolites (Fig. 3). Increasing the stability distance results in thicker and less bifurcate columns merging to massive morphologies. Increasing the attraction distance leads to more space in between columns.

3.4.2. Growth mask (cellular automata)

The automaton used in this paper consists of a kind of an 'evolution mask' that combines all the transition rules. These rules define the relative position between an active cell at time t and the other cells that will be influenced by this active cell in time $t+1$ (Pattisina, 2003; Verrecchia et al., 2004). The growth mask describes a deterministic-type evolution when a daughter-cell state at time $t+1$ results from the mother-cell state and transition rules at time t. A probabilistic-type of evolution is expressed when the state at time $t+1$ is randomly drawn among a set of possible states (Fig. 2A). Therefore, configuration of transition rules inside the growth mask determines the new daughter-cell position after evolution of an active mother-cell.

3.4.3. Substrate and sedimentation/inhibition

The model includes the possibility of modifying the substrate morphology in order to investigate the impact of smooth or rough substrates on build-up growth and morphology. According to the parameters chosen for the simulation, the roughness of the substrate will be enhanced, kept unchanged, or buffered during edifice growth. The simulation can be initiated from a continuous surface as well as from two spots in order to generate growth from a limited surface of initiation.

In the DLA–CA model, two different types of sedimentation are proposed. The first one is part of the DLA process. Because particles are following a Brownian motion, they can be interpreted as chemical or particulate nutrient or physical grains, as stromatolites result from precipitated or agglutinated processes, respectively. This type of sedimentation can be defined as background or normal sedimentation, and can vary with time. Another type of sedimentation is introduced in the model in order to simulate potential disturbance in the stromatolitic construction by various inputs of sediment. This 'catastrophic' burial creates disruptions in the continuum of the active growing surface that have

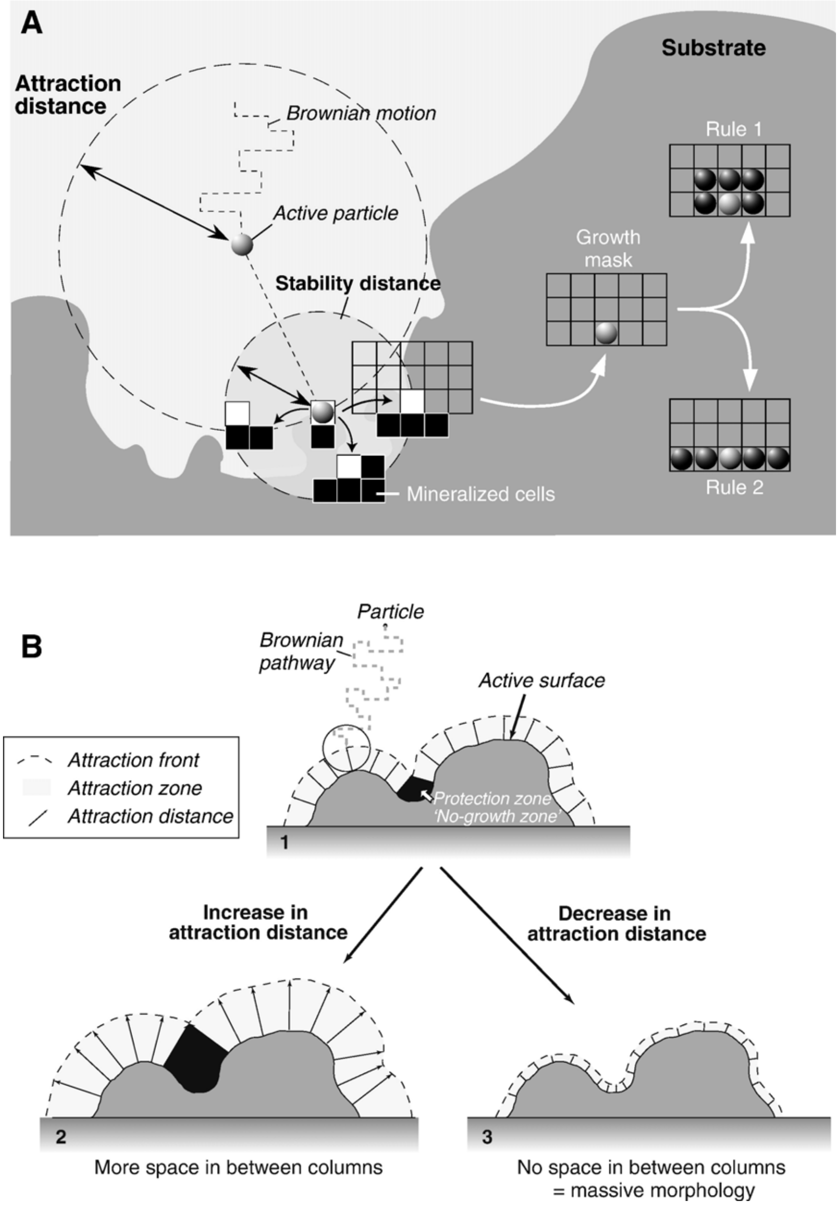

Fig. 2. Main variables used in the DLA–CA model. (A) Illustration of the *attraction distance*, the *stability distance*, and the cellular automata as used in the DLA–CA model (see text for explanation). (B) The overlapping of two attraction vectors leads to the formation of a protection zone, where no growth is recorded. Increasing the *attraction distance* produces more columnar or branching shapes, whereas a decrease provides more massive morphologies.

decisive influence on the global morphology (e.g., ramification). Massive sedimentation can act to randomly inhibit the stromatolite growth. Part of the active surface will continue to grow, whereas several cells are deactivated. Inhibition of active surface cells can have other causes, such as grazing of the active surface, or disease. For this reason, the model proposes an inhibition parameter, which randomly deactivates cells from the surface.

3.4.4. Motion index

This last parameter introduces a control on the Brownian motion of the particles in the DLA process. The *motion index* influences the vertical dimension of the motion, forcing the particle to go down faster in the grid. The particle makes contact sooner with the aggregate and, thus, allows optimization in simulation time. A very high motion index will force the particle to follow a more or less ballistic (straighter) motion,

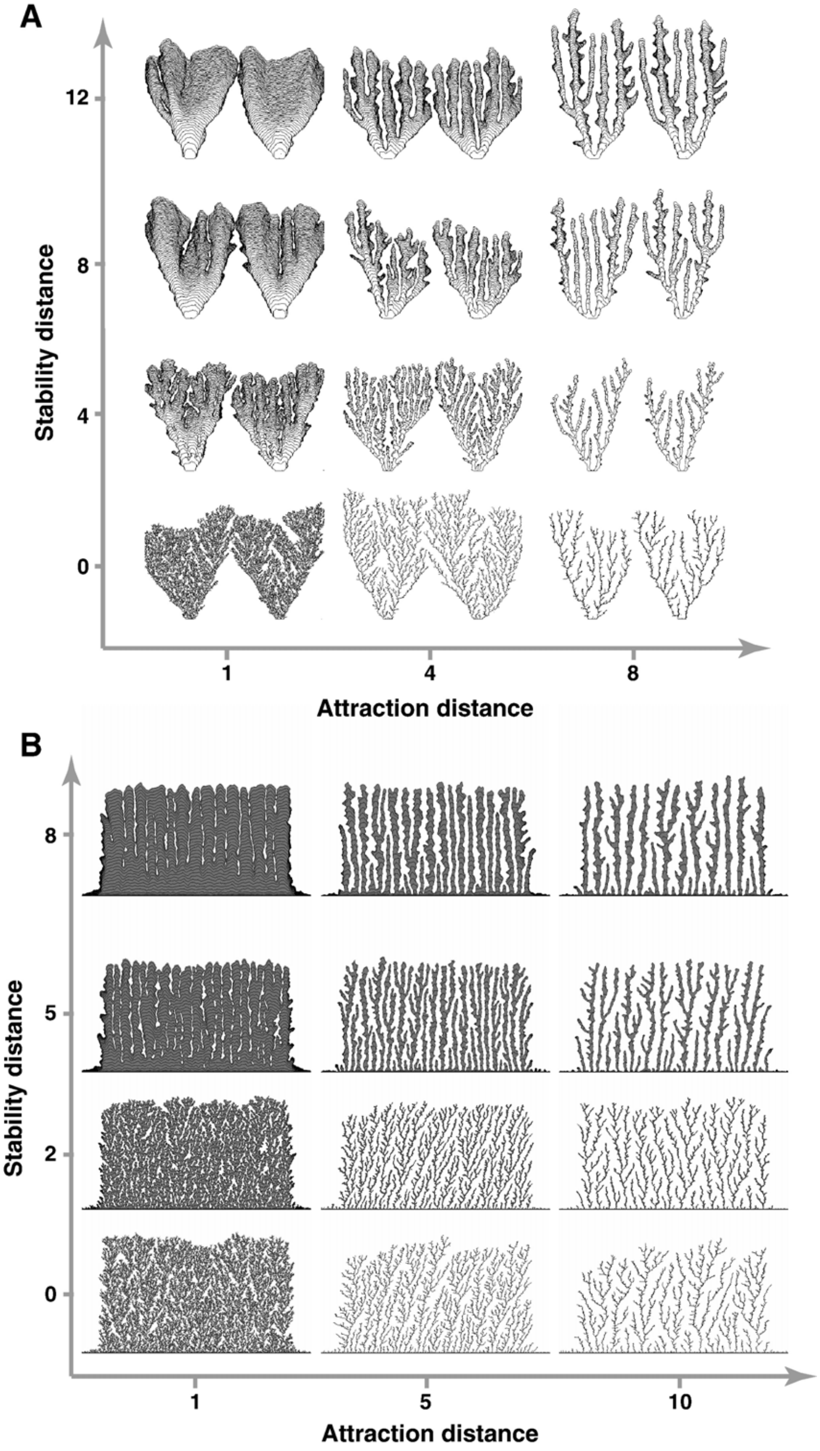

Fig. 3. Result of DLA–CA model simulation showing a variety of stromatolite shapes. (A) The variation in stromatolite morphologies (from massive to dendritic) initiated from two limited areas of growth can be simulated using a minimal number of holistic variables. (B) Comparable simulation using a continuous flat line as initial growth substrate.

whereas a low index will induce conventional Brownian motion. This variation directly affects the final morphology as illustrated in the example below.

4. Examples of simulation

Most significant deposits of Recent stromatolites such as Shark Bay (Australia) and The Exuma (Bahamas) generally display fairly simple massive and domal morphologies. The complexity in morphology noticeably increases when other sources of stromatolites such as hypersaline lakes or freshwater travertine are included. However, this complexity fades in comparison to the one observed in the fossil record, especially in the Precambrian. A large part of these stromatolites shows complex columnar and branching morphologies. Previous numerical models, such as the KPZ equation, fail to simulate morphologies more complex than stratiform or flat domal. The following simulation examples illustrate that a model including intrinsic (local) and extrinsic (environmental) parameters such as the DLA–CA model can produce complex columnar and branching shapes. In addition, the DLA–CA model is able to simulate these morphologies using a very limited amount of parameters (concise and holistic approaches).

4.1. Modern stromatolites

Good examples of morphological evolution of microbialites (stromatolitic and thrombolitic fabrics; Burne and Moore, 1987) are given by biogenic calcium carbonate deposits in Storr's Lake (San Salvador, Bahamas). Different sectors of this hypersaline lake display various build-up morphologies (Mann and Nelson, 1989), i.e., centimeter-size *Scytonema* (filamentous cyanobacteria) knobs in the shallow southern part of the lake (Fig. 4A, B) and larger head-like structures showing alternation of laminated (stromatolitic) and clotted (thrombolitic) fabrics (Fig. 5C). The *Scytonema* knobs grow on irregular substrates (sediments or Pleistocene bedrock) and result from microbially-induced in situ precipitation of high-magnesian calcite. The initial knobs are good examples of more biogenically-

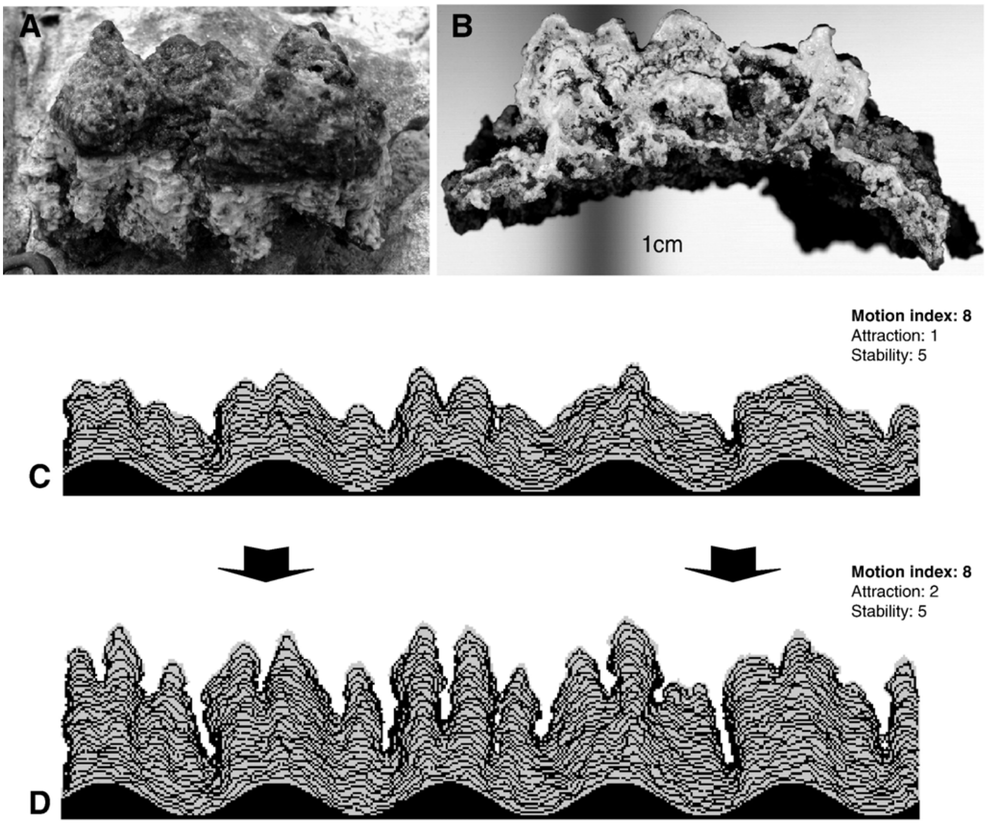

Fig. 4. Simulation of *Scytonema* knobs (San Salvador, Bahamas). (A) Picture of centimeter-size stromatolitic knobs. (B) Section of knobs showing columnar morphologies. (C) DLA–CA simulation showing the columnar morphology as an emergent property. (D) Simulation using slightly different parameters and showing more developed columnar shapes. The *motion index* set at 8 simulates a relative 'ballistic behavior' for the falling particles.

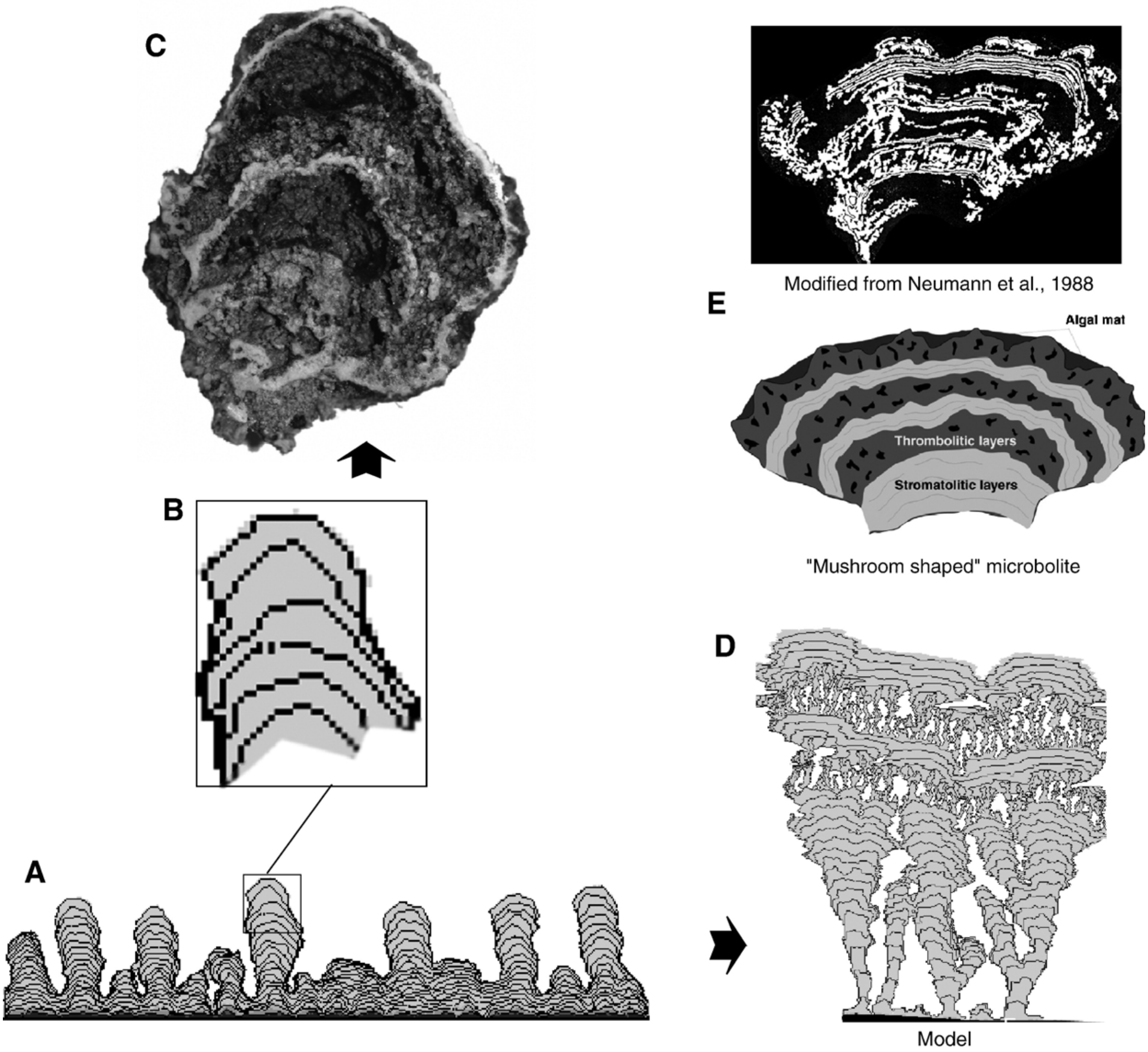

Fig. 5. Environmental control on stromatolitic knob growth. (A)–(B) The evolution of the simulation shows emergent irregularly-spaced lamination during the growth of the simulated knobs and this, without modification of the initial parameters. (C) This irregularity in the simulated lamination is comparable to what is observed in the real knobs. (D) Simulation of the alternation of thrombolitic and stromatolitic fabrics using DLA–CA model. The change in fabrics is obtained by modifying the *motion index* and the *stability distance* allowing the simulation of alternation between heterotrophic (thrombolite) and autotrophic (stromatolite) dominated communities (see text). (E) Drawing made by Neumann et al. (1989) and based on real samples showing this alternation.

controlled morphologies, as *Scytonema* filaments are organized in a fan-like framework that creates pustular or cup-shaped forms.

Simulations shown in Fig. 4 are obtained by setting the *stability distance* to 5, the *attraction distance* to 1 (Fig. 4C) and 2 (Fig. 4D), and by using a rugged substrate. Since calcium carbonate precipitation is indirectly linked to light-driven cyanobacterial growth, the *motion index* is set at high position (8) in order to model energy flux coming from the sun. Following an initial phase of pseudo-columnar growth (massive growth that shows successive crests forming a column-like structure; Walter, 1976), the model slowly produces more individual columns, which display irregularly-spaced laminations (Fig. 5A, B). Similar development is observed in natural ecosystems, where knobs, with regular and tight lamination, develop highly irregular and larger-spaced lamination with time (Fig. 5C).

The alternation of thrombolitic and stromatolitic fabrics (see Kennard and James, 1986) can also be simulated with the DLA–CA model. The origin of the thrombolite in Storr's Lake is still speculative; however, one hypothesis involves changes in physico-chemical composition of lake water through periodic flooding of freshwater (Neumann, oral com.). The stromatolitic sections of the heads record the 'normal' conditions, whereas thrombolitic parts are related to changes in water column conditions. The drastic rise in bathymetry is linked to an increase in water column turbidity through terrigenous input. The translation of this phenomenon is a shift in microbial communities from a phototrophic-dominated (filamentous cyanobacteria *Scytonema*) to a more 'heterotrophic'-dominated community (in this case, coccoid communities). It is important to point out that thrombolite can also be formed by filamentous bacteria (e.g., Moore and Burne, 1994). In the simulation, stromatolitic parts of the build-up are represented by a stable community (high *stability distance*), with a tendency to grow laterally (horizontal CA), and especially a light-driven community (high *motion index*, ballistic motion). The community responsible for the thrombolitic parts is dominated by less light-dependent organisms that do not need to laterally expand on the substrate in order to collect the maximum amount of the sun's energy. Nutrients coming from the water column have a Brownian motion (low *motion index*) and the *stability distance* is smaller. The result is a dendritic, clotted fabric exactly as observed in the natural ecosystem. By alternating the two sets of parameters, similar macroscopic features described in the large Storr's Lake heads can be reproduced (Fig. 5D). The DLA–CA model even allows the simulation of microbialite development from small cm-sized knobs to larger heads, which periodically vary from thrombolite to stromatolite fabrics (Fig. 5D). This development is not directly observed in nature, but it is strongly suggested.

Because the DLA model is based on the notion of self-similarity, this model can simulate morphologies at various scales (giving it a fractal property). Fig. 6 illustrates the accretion mechanism of a modern cm-size *Scytonema* knob at microscopic scale. The lamination observed in these knobs results from changes in filament growth orientation that are seasonally-driven (Monty, 1976; Monty and Hardie, 1976; Freytet and Plet, 1996). Horizontal filament growth (stage 1) is characterized by a large amount of carbonate precipitation (micritic microfabric with ghosts of horizontally oriented filaments, Fig. 6A), whereas vertical filament growth (stage 2) is related to rare precipitation and well-developed porosity (Fig. 6B). The simulation presented in Fig. 6C is only based on modification of the *cellular automata* mask that alternates from horizontally to vertically orientated patterns. The aim is to translate the intrinsic variation observed in the mat with intrinsic parameters of the DLA–CA model, i.e., the *cellular automata*. The result is very close to natural observations.

4.2. Fossil stromatolites

Fossil stromatolites rarely preserve remains of the microorganisms responsible for their formation (see review in Grotzinger and Knoll, 1999). The proof of their biological origin is often based on a single piece of evidence: the lamination. Grotzinger and Rothman (1996) illustrated the formation of abiotic stromatolites through a simple non-linear equation (KPZ equation), hence forcing the scientific community to look beyond lamination criteria to certify the biologic origin of stromatolites. However, the KPZ equation is not able to produce columnar or branching as well as highly porous morphologies. The following examples of simulation illustrate the potential of the DLA–CA model to simulate complex morphologies. In addition, they bring pieces of evidence that such morphologies are difficult to produce without interactions of extrinsic and intrinsic factors, i.e., indirect or direct biological (or organic) control.

4.2.1. Precambrian morphologies

The morphological space of branching and columnar morphologies of Precambrian stromatolites was investigated through simulation with the DLA–CA model. Some results are presented in Fig. 7. The main groups of branching morphologies defined in the literature (e.g., Donaldson, 1976) are simulated by tuning the different parameters provided by the DLA–CA model. By playing with different substrates, the simulation can produce digitate branching morphologies of Gymnosolenid from a limited substrate of initiation (Fig. 7A). Ragged outlines of individual branches (*Jurusania*, Fig. 7B) are obtained by setting the attraction and stability distances to 6 and by enhancing the vertical component of the cellular automata (CA). The divergent branching effect of the Tungussid group results from an increase in the *attraction distance*, an average *stability distance* and an amplification of the CA horizontal component (Fig. 7D). The stubby branching characteristic of *Baicalia* is an emerging property when the *stability distance* is set to 3 without further changes (Fig. 7E). Thus, most Precambrian stromatolite morphologies im-

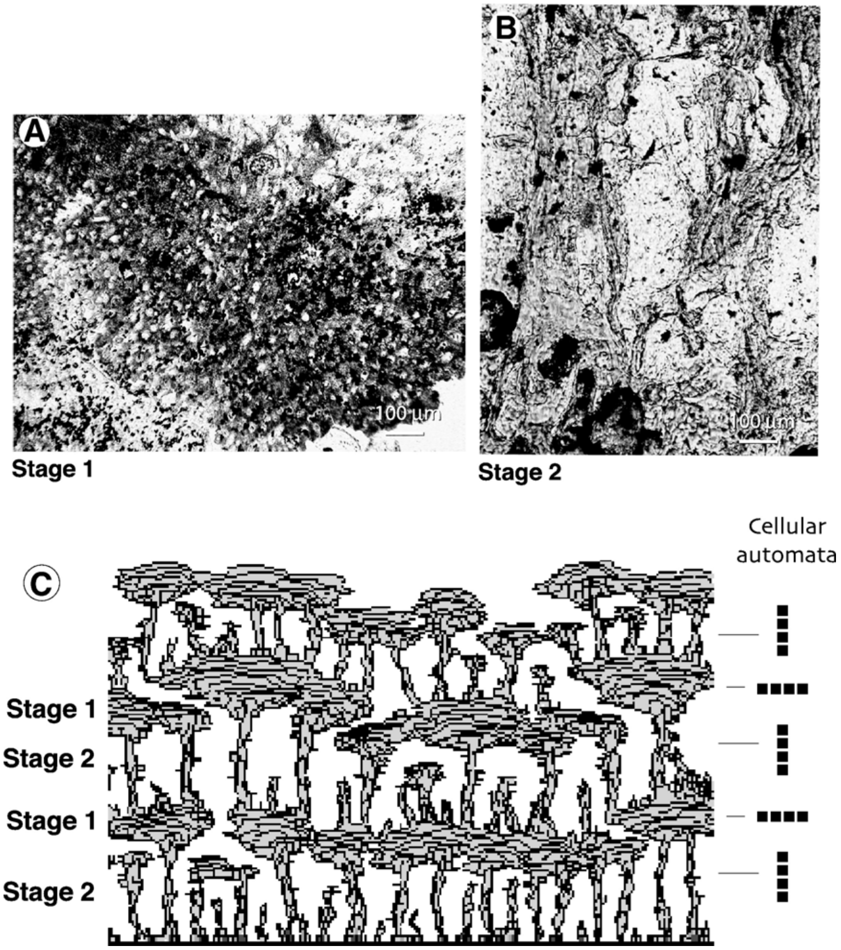

Fig. 6. Illustration of role of the CA component. (A) Thin section photomicrograph of a laminated knob from Storr's Lake (San Salvador, Bahamas) showing a lamina with horizontally-oriented cyanobacterial filaments (holes are molds of cyanobacteria). (B) Same thin section illustrating a lamina with vertically oriented filaments. (C) The alternation in filament growth orientation is obtained by modifying the growth mask of the cellular automata (horizontal and vertical). No other changes have been made to the parameters during simulation.

possible to produce with numerical modeling such as the KPZ equation can be simulated with the DLA–CA model and this, with a minimum number of variables.

4.2.2. Sedimentation impact on Precambrian stromatolite morphology

Precambrian stromatolites were often described with the Linnean binomial nomenclature because the Russian school used stromatolites for biostratigraphy (e.g., Semikhatov, 1976). Many species or even genus names are morphological variations of the same build-up, responding to changes in environmental conditions (e.g., sedimentation or bathymetry). A great deal of columnar morphology observed in natural ecosystems is not the result of a 'genetically programmed behavior', but rather caused by disturbance (disruption of the mat) through external factors. Examples of active disturbances by grazers or dwellers are described in the literature (e.g., Akpan, 1991; Lamond and Tapanila, 2003). However, these factors cannot be invoked in Precambrian times when no such multicellular organisms were present. Sedimentation is often considered as one of the most important agents responsible for morphology. So far, no numerical model has been able to reproduce such a mechanism. The simulation presented in Fig. 8A shows the development of a flat-laminated massive stromatolite that is subjected to a progressive increase in sedimentation. As a function of increasing the sedimentation rate, various branching morphologies emerge from tightly ramified forms to more widely spaced branches. The parameters of the model (indexes and distances) are kept unchanged during the simulation. Interestingly, morphologies obtained between 15% and 25% of sediment can be closely related to the

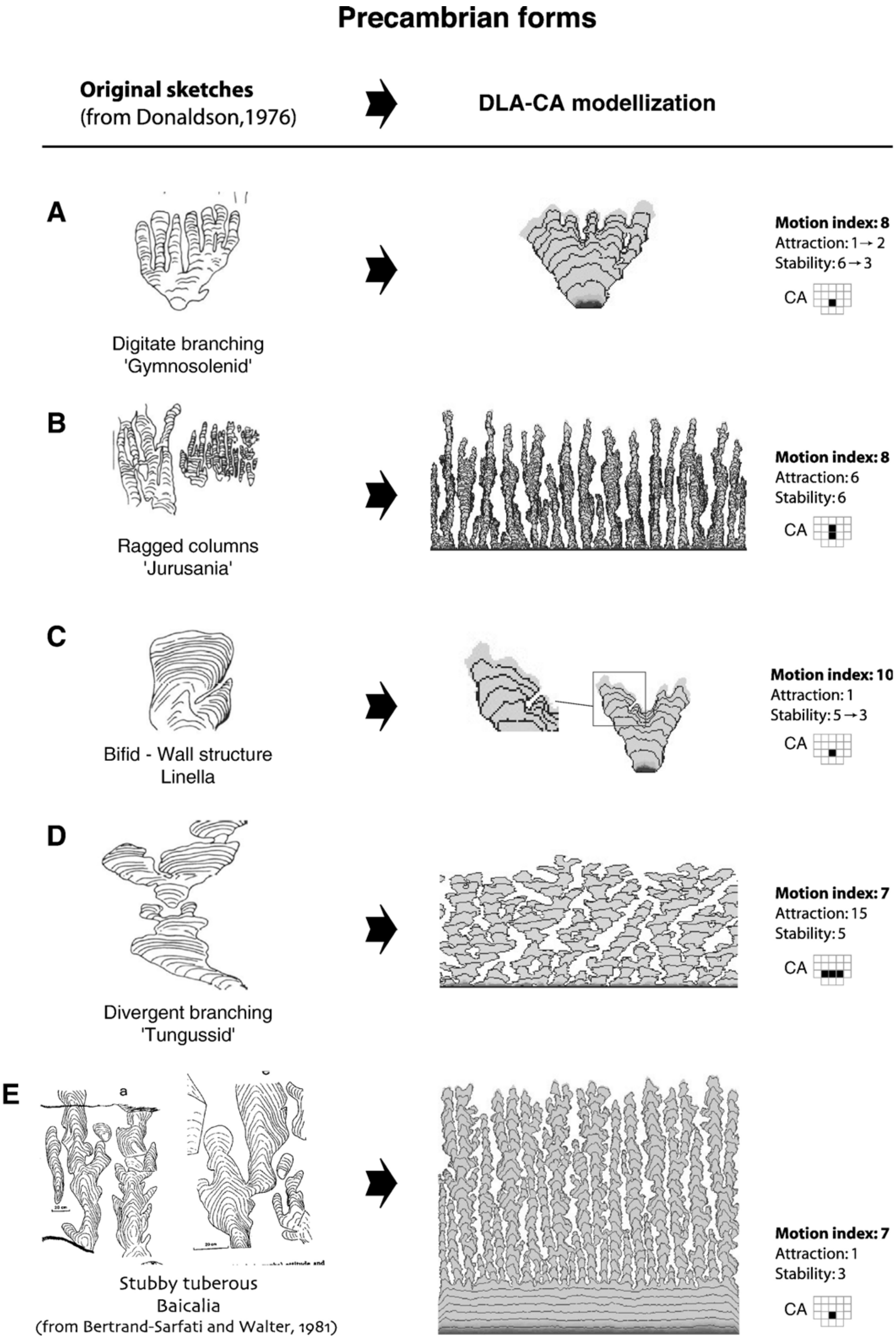

Fig. 7. Simulation of Precambrian stromatolite morphologies using DLA–CA model. See text for explanation (original sketches from Donaldson, 1976).

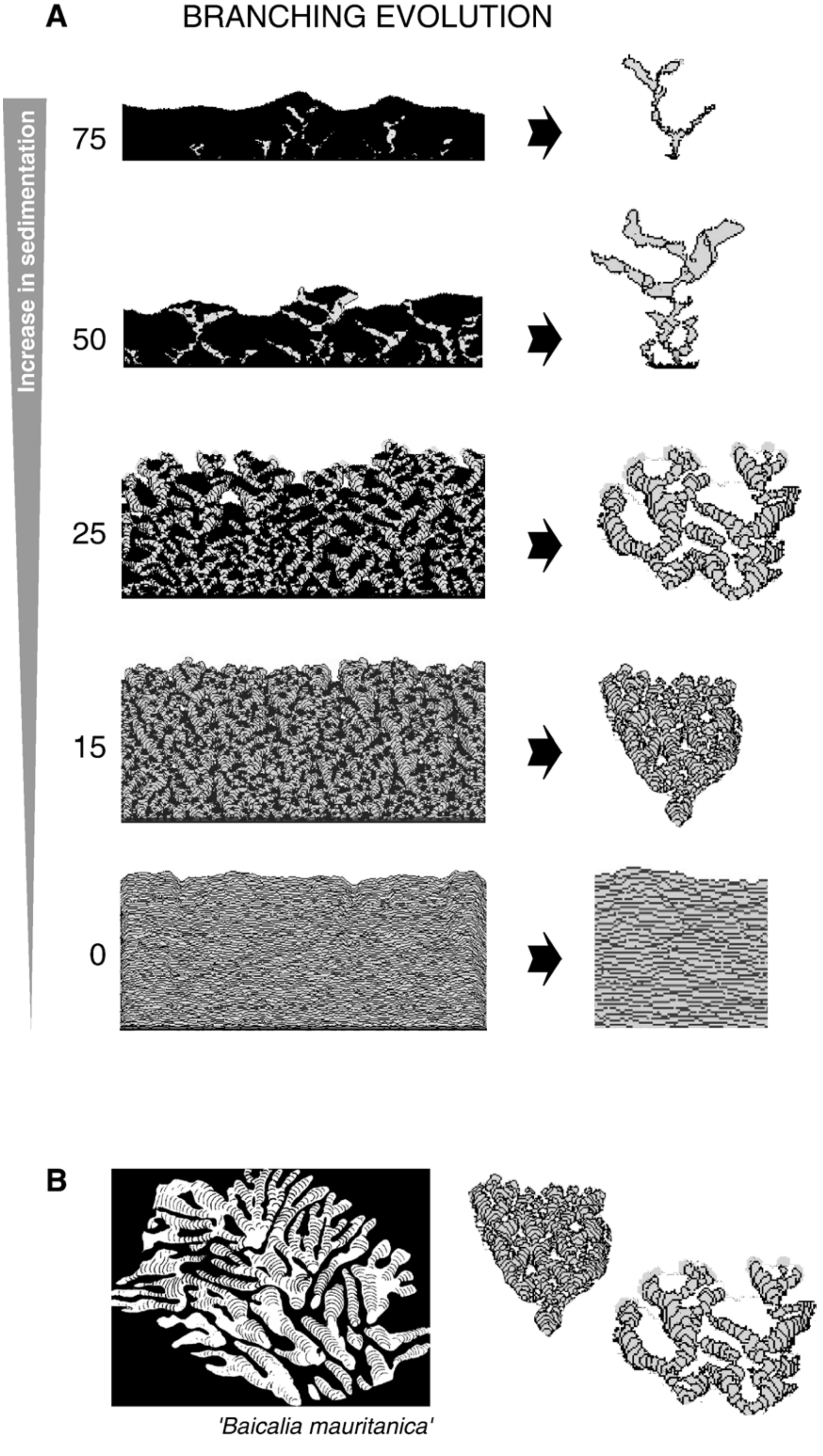

Fig. 8. Effect of the sedimentation on stromatolite morphology. (A) Modification of the branching morphology of stromatolites as a function of the sedimentation. No modification is performed in the parameters during the simulation. (B) A simple increase in sedimentation rate can create branching stromatolites from a massive initial form, resulting in a morphology that looks like *Baicalia mauritanica*, for example. Extrinsic factors can considerably change stromatolite morphologies. Consequently, the use of morphology to assess stromatolite diversity can be questioned.

branching Precambrian stromatolites *Baicalia mauritanica* (Fig. 8B). So, emerging branching morphologies produced through iterative growth of disrupted planar microbial mats can easily be tested with the DLA–CA model.

4.2.3. Environment and morphology

Morphologies are often used to obtain information about environmental growth conditions as well as overall diversity, with the initial assumption that similar environmental conditions would shape similar morphologies (Bertrand-Sarfati, 1994). Simulation using DLA–CA allows such assumptions to be tempered. As shown in Fig. 9, similar morphologies can be simulated using different sets of initial parameters, emphasizing the fractal aspect of the model and, by extension, of the stromatolites. Thus, morphological description is a tool that must be used with great care in order to (1) describe stromatolite diversity and (2) directly translate environmental conditions into morphogenesis.

5. Discussion and conclusions

DLA–CA simulation emphasizes the importance of microbial mat trophic structure on the microbialite morphology. The holistic approach does not produce a detailed mechanistic description of the stromatolite formation but rather a translation in simple parameters of (1) the way that energy, nutrients, and sedimentary particles reach the active surface of a future build-up, (2) how these elements are distributed and used in order to create morphology, and (3) how simple environmental parameters, such as sedimentation, can disturb mor-

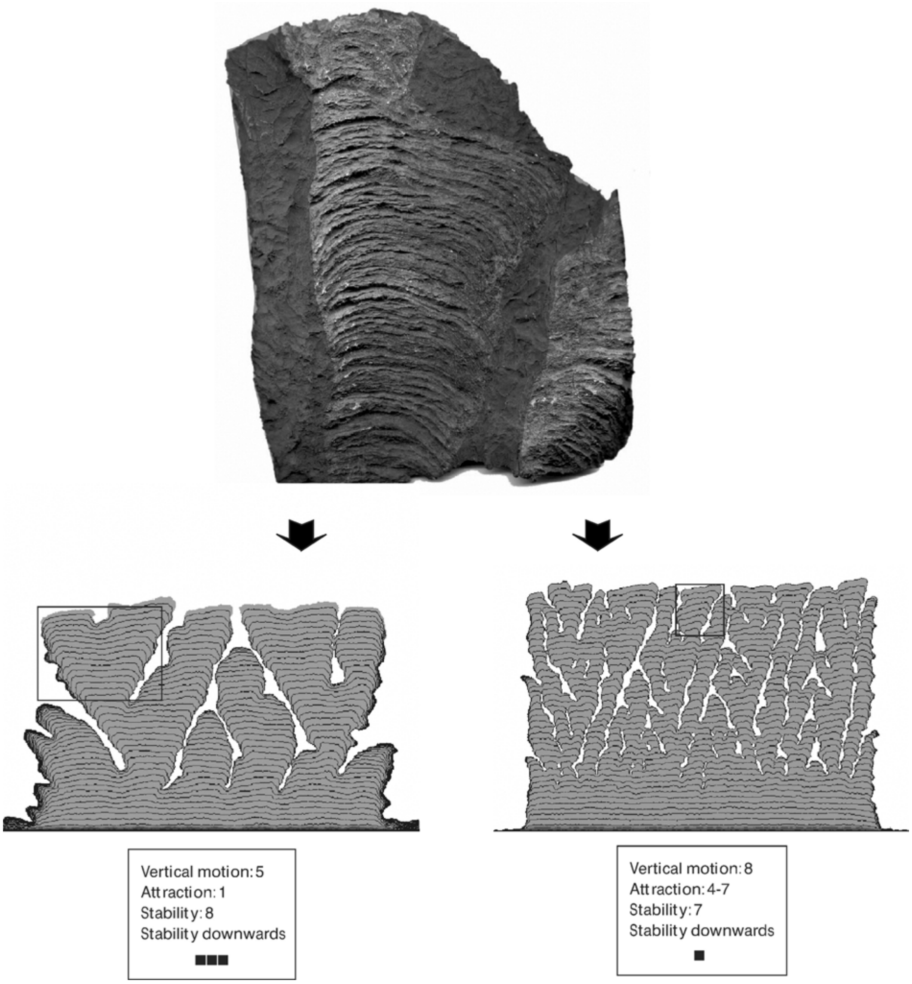

Fig. 9. Fractal property of stromatolites. Similar morphologies can be obtained using very different sets of initial parameters. In accordance with this result, morphology has to be interpreted with great care in order to assess stromatolite diversity and environmental conditions of deposits.

phogenesis. It is possible to achieve morphogenesis through interactions between non-local DLA and local CA models. Indeed, the way particles and/or energy reach the substrate can dictate the overall morphology, whereas emerging changes acquired over time can induce drastic modifications of this overall morphology (Fig. 7). The path followed by particles can be translated, for example, in the different ways in which organisms obtain energy and carbon (phototrophs versus heterotroph). Several examples have been provided in the background section in order to illustrate the relationship between lamina morphology responsible for the overall morphology and the microbial community. The succession of different communities at the top of modern marine stromatolites is responsible for laminae formation (Reid et al., 2000). However, more radical changes in environmental conditions can generate important variations in microbialite types. The model is apparently in accordance with the interpretation that, for example, thrombolite deposits observed in modern microbialites (e.g., Storr's Lake) and in large amounts in fossil coral and sponge reefs (e.g., Leinfelder et al., 1993; Camoin and Montaggioni, 1994; Camoin et al., 1999; Dupraz and Strasser, 1999, 2002) can result from the activity of dominant shade-loving communities using heterotrophic metabolisms, whereas, most massive regularly laminated morphologies (stromatolites) are dominated by light-dependent microorganisms. Manganese dendrites are an extreme example of random aggregation of particles with no relaxation, typical of abiotic construction (e.g., Vicsek, 1992; Barabasi and Stanley, 1995; Pelcé, 2000).

As nutrient/energy reach the top of the build-up, further distribution through the active surface is also a key element of morphological development. As an example, DLA–CA simulations of branching morphologies can result from the decrease in relaxation potential of the microbial mat (surface) related to a smaller *stability distance*. In the case of maximum relaxation (very high *stability index*), the highly efficient redistribution of energy and particles received by the active surface will result in damping of substrate topography, whereas a lack of relaxation translates into a heterogeneous redistribution of this energy and enhancement of small irregularities of the substrate. This mechanism is enhanced by an increase in *attraction distance* that will be efficient enough for column and branch formation with a highly irregular substrate or as soon as topography is created. Thus, high sectors of the mat that get more particles and energy will grow faster than low depleted sectors of the active surface. For example, shadowy areas of microbial mats that grow on highly irregular substrates will receive less light energy than exposed sectors. Following this idea, the self-organization of *Scytonema* filaments that is responsible for the production of small columnar knobs (see above) may be an optimization of the access to solar energy. However, too strong an exposure can result in opposite consequences, as sectors of highly exposed microbial mat can also shut down their photosynthetic activity when solar irradiation is too high (e.g., Powles, 1984; Andersson and Barber, 1996).

On the other hand, most columnar or branching morphologies observed in fossil stromatolites are not the result of such mechanisms. Microbial mats cannot be compared with trees or coral reefs, which are genetically programmed to produce specific microstructures and morphologies. Precipitation in microbial mats is mostly induced and the mat will need external disturbances (disruption of the mat) in order to initiate morphologies. Partial burial by sediment remains one of the most important agents responsible for columnar formation. The model attempts to prove that morphology does not seem to be a good indicator of stromatolite diversity, as different sets of intrinsic and extrinsic parameters can produce similar morphologies. Although important changes in microbial community composition can initiate changes in microbialite morphology, stromatolites (one type of microbialite) show a wide range of morphologies that are not necessarily related to modification in community surface. The morphological space of the stromatolites can mainly be investigated through external disturbance on the same mat.

Although the model gives some insight into the complex interaction between intrinsic and extrinsic factors responsible for stromatolite growth, it only represents a first step in the use of holistic modeling of stromatolites and other natural morphological expressions. For example, the intrinsic part of the model remains oversimplified. The cellular automata offers an interesting but rather reduced idea of what really happens in the microbial community cycle responsible for laminae formation. Indeed, the model does not produce a mechanistic description of the laminae but rather a holistic approach to morphology generation. Future steps in the research could include more information about processes related to stromatolite formation by using some kind of 'artificial intelligence' approach, such as multi-agent platform (Dommergues et al., 2004) that will allow a better characterization of both intrinsic and extrinsic factors responsible for stromatolite growth.

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