STUDIA GEOLOGICA POLONICA
Vol. 124, Kraków 2005, pp. 143–157.
Methods and Applications in Micropalaeontology
Edited by J. Tyszka, M. Oliwkiewicz-Miklasińska,
P. Gedl & M. A. Kaminski

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State-of-the-art in modelling of foraminiferal shells: searching for an emergent model

(Figs 1–7)

Abstract. Modelling of foraminiferal tests (shells) started from the fixed-reference models, which used fixed points or axes as coordinate systems. Simulated shells are limited to simple planispiral, trochospiral or uniserial shell patterns, stable throughout ontogeny. On the other hand, various groups of foraminifera change chamber arrangements during their growth. Modelling of more complex forms, with changing chamber arrangement patterns, requires apertures, which are essential for morphogenesis of foraminifera. The moving reference model has solved this requirement, including apertures as reference points. This approach gives morphogenetic priority to apertures and produces more realistic simulations. Nevertheless, these models are still not ”deep” enough to reflect the complexity of foraminiferal shells. It is proposed to focus on morphogenesis of real foraminifera and go deeper into the processes responsible for chamber formation. Earlier studies have shown that the cytoskeleton plays a major role in shaping the chambers. A new emergent model should introduce intracellular dynamics during the chamber formation. Internal processes should rather mimic physical interactions and biochemical reactions than geometric transformations. The foraminiferal morphogenesis ought to emerge spontaneously from simple rules and parameters, instead of being predefined in the form of geometric figures and their transformations. The Diffusion Limited Aggregation (DLA) model, presented here, tests such a new emergent approach.

Key words: theoretical morphology, foraminifera, morphogenesis, self-organization, simulation, Diffusion Limited Aggregation (DLA).

INTRODUCTION

Foraminifera (Order Foraminiferida Eichwald) are unicellular organisms, which typically build mineralised or organic-mineralised tests (shells). They are easily fossilizable and show very high variability in time and space, which makes

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them perfect targets for biostratigraphic, palaeoecologic, palaeoceanographic, and palaeoclimatologic studies. Tests of foraminifers show a nearly endless diversity of shapes and patterns, and can be divided into 3 informal groups, corresponding to the trend of increasing shell complexity, from unilocular tests, through simple multilocular forms to complex tests with subdivided chambers (chamberlets) and/or complex wall structures. In contrast to unilocular and most of tubular forms, multilocular tests enlarge chamberwise, i.e. in discrete growth steps by the process of chamber additions successively united into the shell during ontogeny (Hottinger, 1986, 2000).

The interest in morphogenesis of foraminiferal tests started with the spectacular monograph of d'Arcy W. Thomson (1919) *On Growth and Form*. The idea of modelling foraminiferal morphogenesis has been undertaken by several authors since the late sixties (see McGhee, 1999 for an overview). Unfortunately, there is still a huge gap between understanding of foraminiferal morphology and the morphogenetic processes behind it. However, our knowledge on the morphology of Recent and fossil foraminifera is substantial, we still do not know how genetic codes are translated into actual chamber shapes and arrangements (Tyszka & Topa, in press). The aim of this paper is to review former models and focus on future prospects of foraminiferal modelling.

STATE-OF-THE-ART

Fixed-reference models

Berger (1969) presented the first formal model, which followed the classical model of macrofaunal shell coiling (Raup & Michelson, 1965; Raup, 1966). The shell in this model is fixed to a point, which defines the so-called centre of the shell (Fig. 1A–C). This point (or axis in other models) is a reference point for all geometric transformations responsible for simulation of shells. The model represents a simple step-by-step rotation of a circle with a certain overlap and expansion of a circle radius (Fig. 1A–C). Resulted theoretical morphospace, including all possible simulated shell patterns, presented two-dimensional planispiral shells, which mimicked a variety of planktonic foraminifera. Successive models followed Berger's approach (e.g., see Scott, 1974; Webb & Swan, 1996). Signes *et al.* (1993) designed a similar model with two basic assumptions concerning foraminiferal growth: the shape of the chambers in the shell remains constant with growth, and the volume of each new chamber increases at a constant proportion to the pre-existing volume of the shell. This model produced isometric growth with coiling in a fixed-reference frame.

Other authors also modelled the allometry of foraminiferal shells. Brasier (1980) who produced a working morphospace model of foraminiferal forms using four parameters, which actually corresponded to Berger's parameters, expanded by the degree of extension of growth along coiling axis and the degree of chamber compression. Although his theoretical morphospace was not further implemented, it brought some new ideas. A further significant contribution to fixed-reference

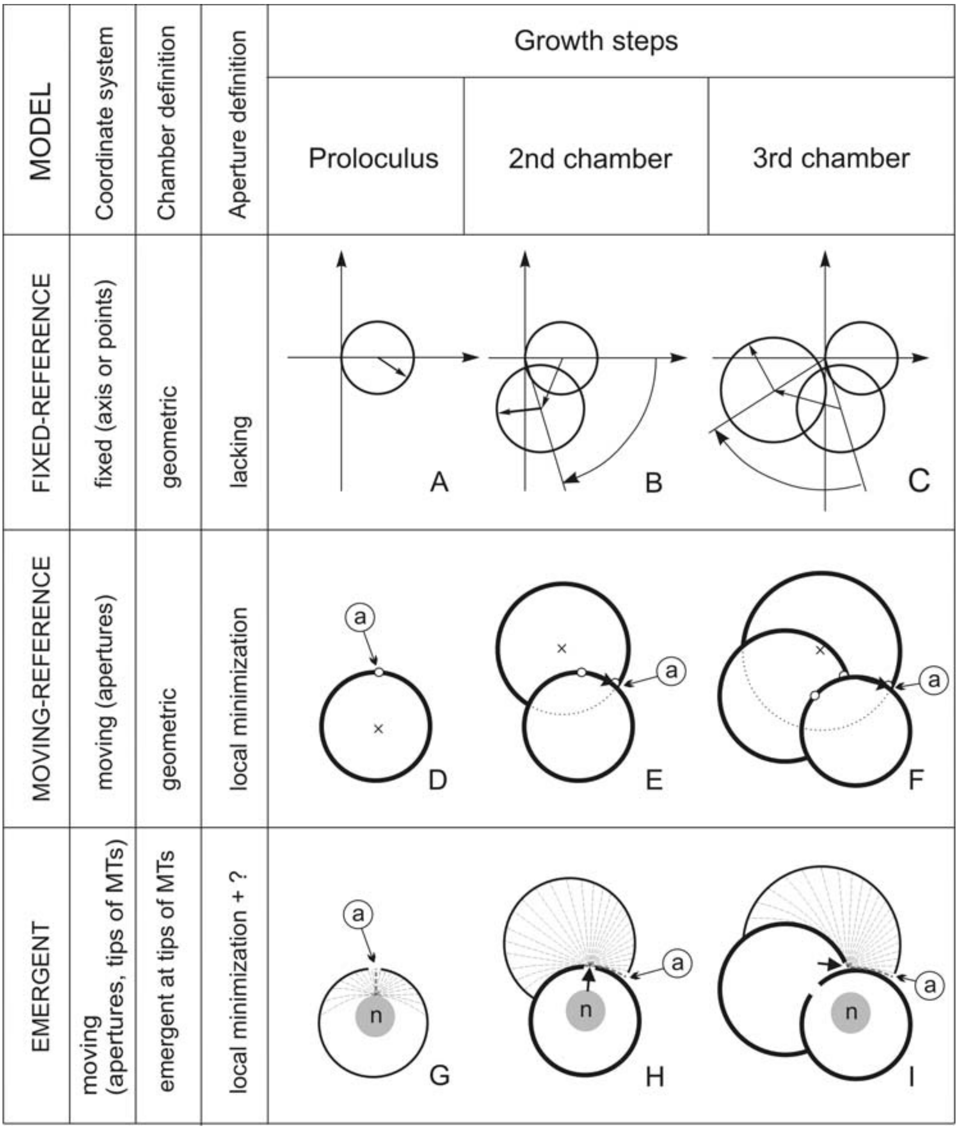

Fig. 1. Models of foraminiferal test (shell) morphogenesis with three steps creating the first three chambers. A–C – Fixed-reference model (after Berger, 1969, modified); D–F – Moving-reference geometric model (after Topa & Tyszka, 2002, modified); G–H – Moving-reference emergent model with fan-shaped rhizopodia (under construction); a – aperture, n – nucleus, MTs – microtubules

models is the logistic approach introduced by De Renzi (1988, 1995) who simulated the allometric growth of five morphotypes of *Alveolina*. Unfortunately, the internal complexity of chambers expressed by small-elongated chamberlets was not considered in the model.

All the above-mentioned models used theoretical axes, which were arbitrarily defined and have no morphogenetic or physiological meaning. These models could simulate pure planispiral, trochospiral or uniserial chamber arrangement, but could not simulate more complex patterns. For instance, they could not model gradual or abrupt changes of coiling axis with different chamber arrangements (e.g., *Spiroplectammina* with planispiral to biserial growth patterns). In spite of an important contribution to modelling, hitherto the fixed-frame models just partly reflect the real morphogenetic variability of foraminifers. Therefore, new more realistic methods of "deeper" modelling based on a better understanding of foraminiferal morphogenesis were essential.

Moving-reference models

The idea of leaving the fixed reference frame in favour of the moving reference frame came from the theoretical morphology of ammonites, plants, and marine sessile organisms. Okamoto (1988) proposed a tube model for all types of shell coiling, including heteromorph forms with abrupt changes of coiling patterns. At each growth step, the aperture migrates from its present position to a new position, according to locally defined rules (Ackerly, 1989). A similar moving-reference frame is used in simulating radiate accretive growth of marine sessile organisms, such as corals and sponges, where the growth axis is associated with the local maximum of growth (e.g., Kaandorp, 1994; Hammer, 1998). Actually, a comparable approach has been used much longer in the simulation of the growth of plants (Lindenmayer, 1968; Prusinkiewicz & Lindenmayer, 1990).

The need for a new approach was already mentioned by Signes *et al.* (1993) who noticed that the foraminiferal "axis of coiling may not be stable and often lacks a physical representation on shells" and mentioned the advantage of local-coordinate models, which describe growth from an organismal vantage point, that is from the aperture". Apertures are essential elements of the tests because they are openings through which pseudopodia (rhizopodia) extrude. Apertures are important for communication of foraminifers with external environment. These openings (foramina) also create an internal communication path via successive chambers. It is clear that apertures have a great impact on the morphogenesis of foraminiferal tests (Topa & Tyszka, 2002; Tyszka & Topa, in press).

The first model, introducing a moving reference system into modelling of foraminiferal tests, was proposed by Topa & Tyszka (2002) and Tyszka *et al.* (2004). It is an iterative model based on a local reference system linked to the foraminiferal aperture and minimization of the local communication path (Fig. 1D–F). Minimization of the local communication path means that the distance between two successive apertures is minimal. This idea partly derives from publications of Hottinger (1978) and Brasier (1982) who noticed that foraminifers tend to shorten distances between the first and last compartments of its shell and concluded that foraminifers show a trend towards minimizing the distance from the back of the first chamber (proloculus) to the most proximal aperture in the final chamber. This global minimization facilitates information transfer from and to the nuclei as regulation centres (Hohenegger, 1999). Verification of this idea let to the conclusion, based on observation of fossil foraminifers, that foraminifers tend to shorten local distance in order to shorten the global communication path (Topa & Tyszka, 2002). Computer implementations of this model show the simulated foraminiferal shells much closer follow real trends in foraminiferal morphogenesis and allow simulations of forms, which were not possible before (Fig. 2) (Topa & Tyszka, 2002; Łabaj *et al.*, 2003; Tyszka & Topa, in press).

Towards an emergent model

The above models are not "deep" enough to reflect complexity of foraminiferal shells. Both of them are purely geometric in nature. Although the second model gave up unrealistic fixed references and introduces apertures as local and moving references, it still uses artificial parameters, such as angles, ratios etc. Another much deeper model is necessary based on simulation of real processes, which take place in the foraminiferal cell. Such a model should still act locally, and there are no doubts that apertures should represent local reference centres around which successive chambers are formed. The foraminiferal morphogenesis ought to emerge spontaneously from simple rules, instead of being predefined in the form of geometric figures and their transformations.

It is supposed that the test morphology is directly defined by the genetic code through the intracellular self-organisation of hierarchical processes stimulated mainly by genotype and partly by environment. Therefore, shell patterns **emerge** from the cascade of morphogenetic processes, controlled by genetic information and external conditions.

In order to describe such a model, we should focus on morphogenesis of real foraminifera and go deeper into the processes responsible for chamber formation. Several culture investigations have been carried out that described chamber formation (for details see Hemleben, 1969; Spindler & Röttger, 1973; Berthold & Spindler, 1978; Bé *et al.*, 1979; Hottinger, 1986; Hemleben *et al.*, 1989). These empiric studies have shown that the cytoskeleton, dominated by microtubular dynamics, plays a major role in the shaping of chambers. According to Hottinger (1986), foraminiferal chamber shape depends on "the length of pseudopodia extruding from the previous chamber combined with the geometry of apertures on the previous apertural face" during chamber construction. Rhizopodial patterns are most likely controlled by microtubular dynamics governed by processes responsible for tubulin polymerization and depolymerization (Hottinger, 1986). Concentration gradients of free tubulin, a protein constructing microtubules (MTs), are essential for localized growth or disintegration of microtubules and complete rhizopodia. It is likely that other molecules, including motor proteins and regulatory proteins, are also critical for these processes. Selforganization of all these components is responsible for overall cytoskeletal dynamics (e.g., Nédélec *et al.*, 1997; Maly & Borisy, 2002).

This new emergent model, proposed herein, should introduce intracellular dynamics during the formation of chambers, including intracellular signalling, forma-

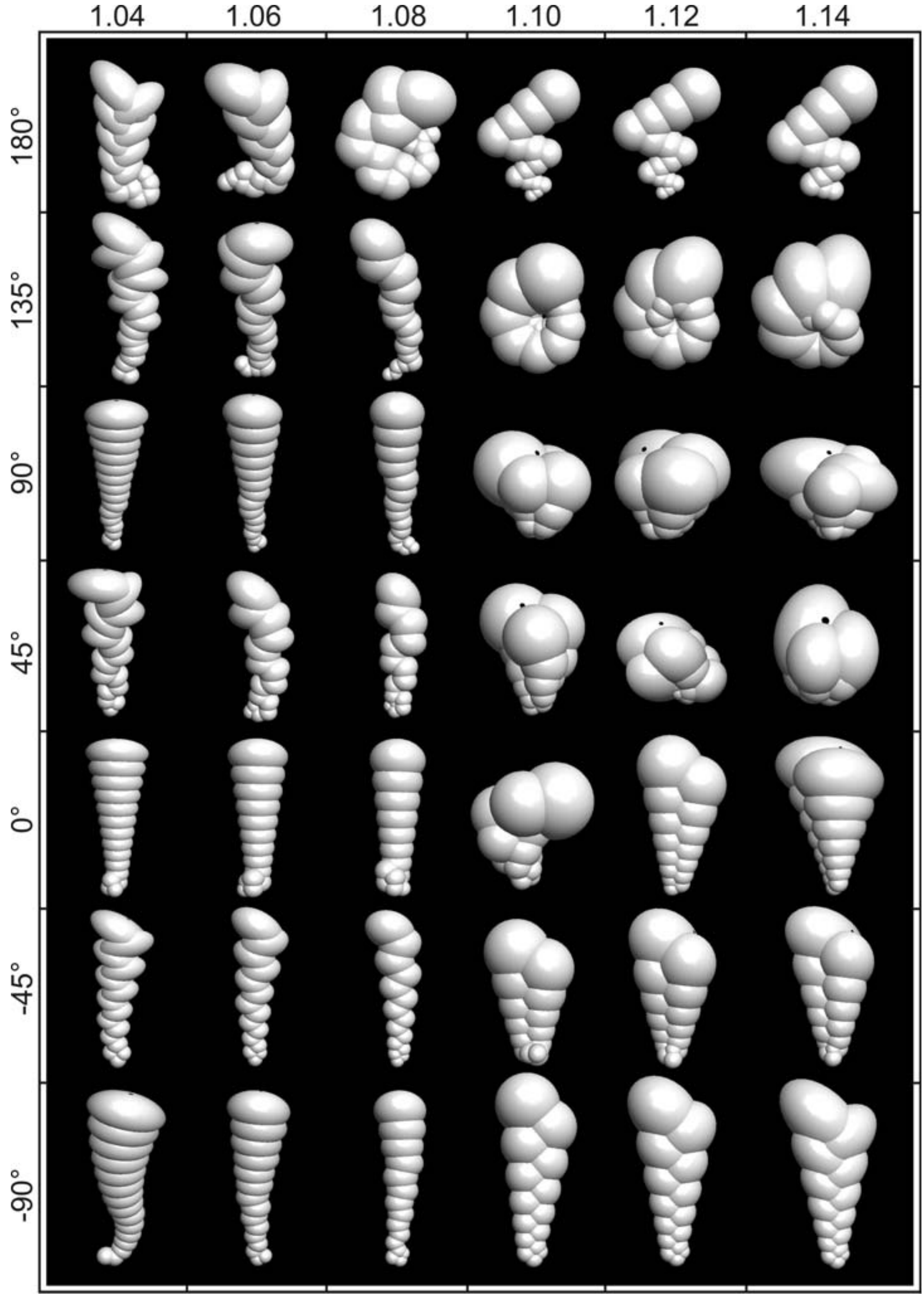

Fig. 2. Fragment of 2-dimensional morphospace of virtual foraminiferal tests (shells) generated by the moving reference model. All 6 parameters are non-random. Two chamber scaling rates are fixed at 1.1. The third chamber scaling rate called "chamber deep ratio", ranging from 1.04 to 1.14, are scaled along the *x*-axis. Deviations of the growth vector, ranging from –90° to 180°, are scaled along the *y*-axis. Scaling rate of the growth vector is fixed at 0.1 and rotation of this vector at 0° (see Łabaj *et al.*, 2002 for further details)

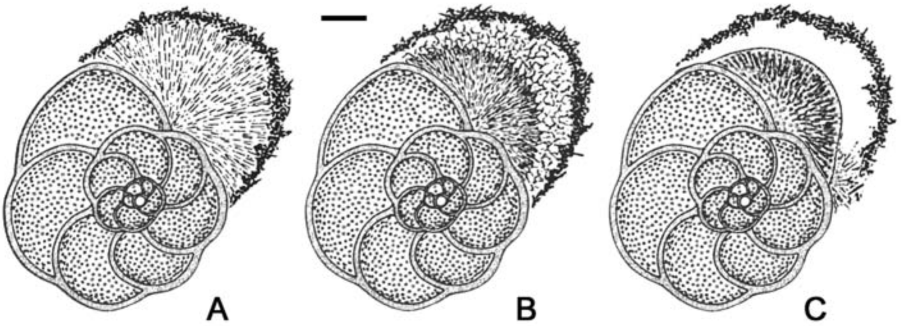

Fig. 3. Formation of a new chamber in *Discorbis bertheloti* (from Grell, 1978, after Le Calvez. 1938, modified). **A** – fan-shaped rhizopodia spreading from the aperture located on the opposite (umbilical) side; **B** – retraction of rhizopodia; **C** – secretion of a new chamber. Scale-bar = 0.5 mm

tion of microtubular networks, the primary organic membrane, 'Anlage', test secretion, formation of aperture/s, pores, external structures, secondary laminas etc. Internal processes should rather mimic biochemical reactions and physical interactions than geometric transformations. The foraminiferal morphogenesis ought to emerge spontaneously from simple rules and parameters, instead of being predefined in the form of geometric figures and their transformations (Tyszka & Topa, in press). Unfortunately, all these processes are very complex; therefore, generalization is necessary to build up a relatively simple and functional model. But fortunately, the model can employ knowledge from recent advances in cell biology and bioinformatics (see Nédélec *et al.*, 1997; Maly & Borisy, 2002).

VIRTUAL EXPERIMENTS WITH DIFUSION LIMITED AGGREGATION MODEL

Methods and preliminary results

The Diffusion Limited Aggregation (DLA) modelling method was introduced by two physicians in 1981 (Witten & Sander, 1981). They were searching for a simple numerical method able to produce fractal-like, dendric structures similar to those observed during the process of electrolytic aggregation.

DLA simulates two physical processes:

– diffusion – particles are walking randomly in space (Brownian motion),

– aggregation – particles attaching themselves to an existing solid structure.

Apart from simulating the growth of dendritic structures, DLA has been successfully applied to modelling other phenomena, such as: coral growth (Kaandorp & Kuebler, 2001; Kaandorp *et al.* 1996), the path taken by lightning (Niemeyer *et al.*, 1984), snowflake formation (Nittman & Stanley, 1986), coalescing of dust or smoke particles (Fedkiw *et al.*, 2001), river networks (Masek & Turcotte, 1993), etc.

There are several methods of simulating the DLA by computer. Perhaps the most common is to start with a white surface except for a single black pixel in the centre. This black pixel represents a still particle as a seed of the structure. New points move from the borders and randomly (approximation of Brownian motion) walk until they get close enough to stick to the existing black pixel. Then they stop walking, attach, becoming a part of the whole structure.

All details of this DLA-model have been presented separately (Saczka, 2004). The model is based on the orthogonal lattice. In order to model the behaviour of foraminiferal rhizopodia, some modifications are introduced. The main goal is to produce branching structures resembling and behaving like real rhizopodia. During chamber formation, rhizopodia form a fan of radial branches spreading from the aperture. Comparing structures generated by the classical DLA model, the rhizopodial networks are denser and regularly cover the fan-like area around the aperture. Moreover, rhizopodia do not have such a rich fractal dentritic pattern as that produced by the classical DLA model.

The following group of modifications takes into account diffusion processes:

1. Excluded area is the forbidden region for particle walking (see Fig. 4). It represents the shape of already existing chambers. The particle which meets the border of this area, reflects or is glued.

2. Internal source of particles. The traditional DLA model assumes that the particle is generated far from the centre of aggregation. In contrast, rhizopodia are constructed from the tubulin particles produced inside the shell and transported outside. This modification assumes that new particles are spread over the area, representing the aperture. The stickiness parameter has to be activated to prevent particles from early gluing.

3. Field of reaction has been introduced in order to reduce the number of small fractal branches that are typical for DLA structures. Each aggregated particle generates a negative gradient of certain quantity in the area nearby. Gradients generated by neighbouring particles accumulate and prevent particles from creating larger groups. The new particles are more likely to be glued to particles with fewer neighbours, because their gradients are not steep enough.

Some of the modifications presented below are connected with parameters that control the process of aggregation:

1. Stickiness (sticking coefficient) controls the process of gluing new particles to an existing structure. If the value of this parameter is too low, the particles cannot be attached, and in consequence, reflect from the structure. Each particle reflection increases the stickiness value. In practice, this modification prevents particles from gluing to the most external part of the structure and makes the final pattern of branches denser.

2. Weight parameter prevents branches from being too elongated. The arbitrary chosen value is initially set in the seed particle and then it is transmitted from the already aggregated particle to the particles that have just been attached. During the transmission the parameter is decremented. A particle with too low value of this parameter cannot aggregate new particles and, in consequence, simply rebounds them.

3. Distance parameter also prevents the model from building too elongated

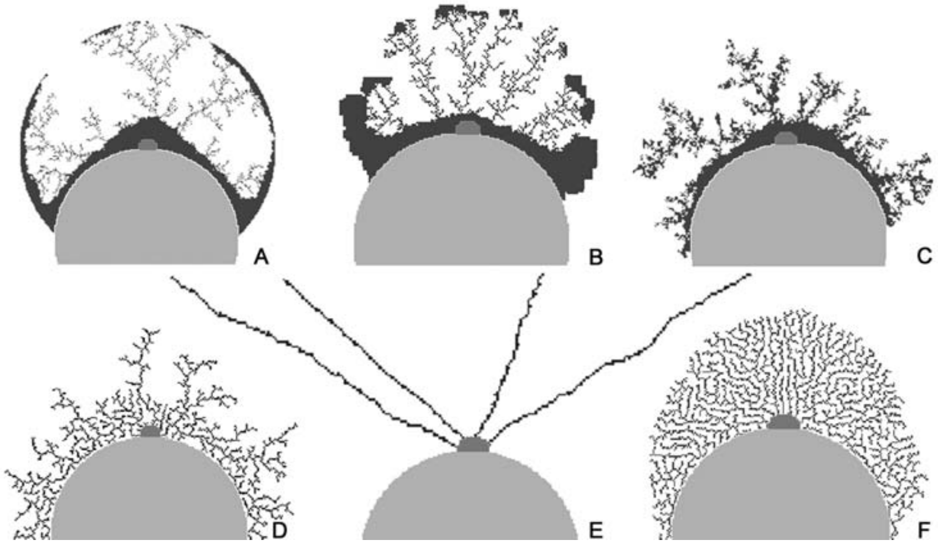

Fig. 4. Formation of a new chamber using the DLA-based model. The pictures illustrate modifications introduced based on the DLA algorithm: **A** – distance parameter; **B** – weight parameter; **C** – stickiness; **D** – field of reaction; **E** – branch growth angle; **F** – field of reaction combined with internal source. Grey circles depict excluded areas representing existing shells with virtual apertures shown as dark crescents

branches. New particles aggregate only within a certain distance from the aperture. As a result we obtain a fan-like network of branches (Figs 4A, 5A–D).

4. Branch growth angle limits the growth angle of every branch referred to the middle of the “seed”, which could be an aperture during chamber formation. This modification is set up to facilitate radial growth of elongated branches.

Combinations of two or more of these modifications have also been applied. The results obtained with various modifications introduced in the DLA model give a very wide variety of patterns (see Fig. 4A–F). Figure 4A–C shows fractal structures presenting, known for instance, from manganian dendrites. These branching structures are either very delicate due to simulation without weight or stickiness modifications (see Fig. 4A) or quite thick (Fig. 4C) applying a high stickiness parameter. All three forms show heavily glued bottoms of created “chambers” attached to the existing “shell”. It is brought about by application of the ‘internal source of particles’. This pattern can be avoided, if we apply ‘external sources of particles (classical DLA-model) or introduce the ‘field of reaction’ (see Fig. 4D–F). The first option is unrealistic because particles represent tubulin molecules, which are synthesized within the cell, either inside the existing shell or within the formed chamber. Tubulin molecules do not diffuse from the outside of the foraminiferal cell.

The ‘distance’ modification (parameter), from first sight, seems to be artificial because resembles purely geometric models with ideal circular chambers. This parameter gives the structure a chamber-like outline (Figs 4A, 5A–D) and may repre-

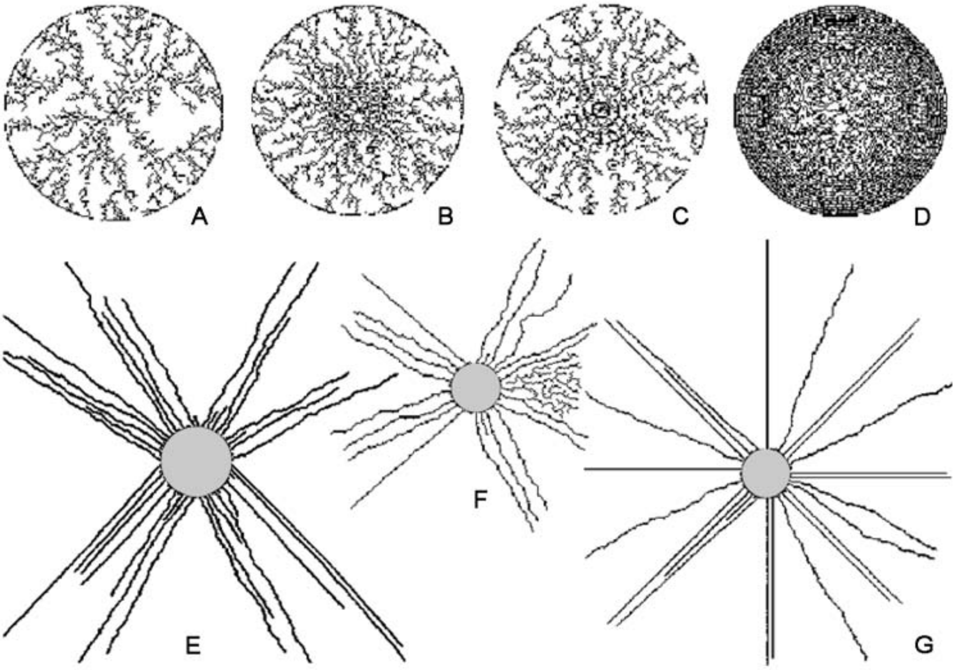

Fig. 5. **A–D** – Radial and circular structures resembling droplet-rhizopodial interactions generated with dynamically changing 'distance' parameters (see Saczka, 2004 for details); **E–G** – Irregular radial rhizopodia-like structures with low 'growth angle' parameters and different values of 'field of reactions'. Margins of grey circles attract attachment of particles in contrast to 'excluded areas' presented on Figs 4 and 6

sent a droplet of cytoplasm, unfortunately, without its fluid-like dynamics. It is clear that this parameter is obviously oversimplified and not emergent.

Actually, relatively narrow ranges of parameters give patterns resembling different types of rhizopodia. Furthermore, the simulated structures are very sensitive to slight changes in the parameters (modifications). The most realistic types are presented on Figures 4D–F and 5A–E, which are simulated with the introduction of the 'field of reaction'. This way we obtain networks of equally located, more or less elongated branches. Elongation of these branches can be modified by the 'growth angle', with the "most elongated" branchless structures (Fig. 4E) to regularly diverging limbs (Fig. 4F). These elongated branchless and intermediate fine networks (Fig. 6A–E) are similar to real single rhizopodia and reticulopodia. In fact, reticulopodia in reality form long thread-like pseudopodia that branch apart and rejoin. Their original structure is therefore anastomosing. The simulated structures are pseudo-anastomosing because these branches do not rejoin (Fig. 6A–E).

It should be stressed that the variety of simulated structures is much broader. An extensive description of this novel approach in foraminiferal modelling and an overview of the results have been presented elsewhere (Saczka, 2004).

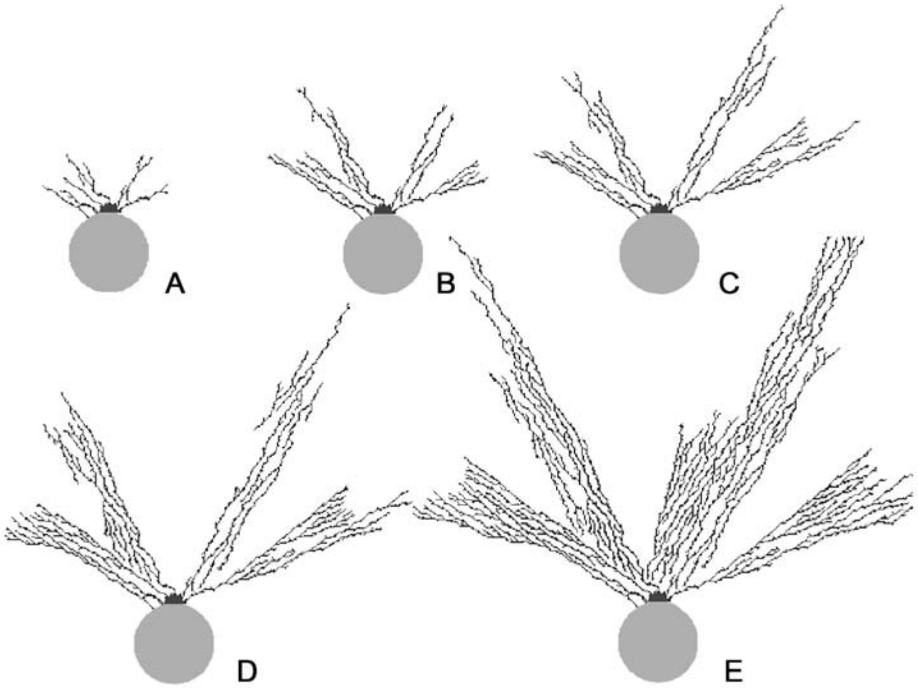

Fig. 6. **A**–**E** – Successive time-laps pictures presenting growth of "reticulopodia" spreading from the virtual aperture (dark crescents). Simulated with the following modifications: internal source of particles, field of reaction from 0 to 3.25; growth angle calculated based the cotangents function with a 0.8 tolerance

DISCUSSION

The presented results (see Figs 2, 4, 5) on the modelling of foraminifera are preliminary, nevertheless, they have shown that moving reference models extended to emergent models are very promising. The presented DLA model follows the moving reference approach because particles attached refer to existing structures. Therefore, the reference frame is represented by all points to which new particles can be adhered, and in result, it moves together with the growing structure. There is no conflict with apertures as reference points because they operate at a higher emergent level. The local minimization paradigm can be introduced as an independent level of reference. This way the overall model gets step by step deeper into morphogenetic self-organisation (see Seilacher, 1991).

Resulted simulations have shown that it is possible to model various states of foraminiferal cytoskeleton, such as "single rhizopodia", "fan-shaped rhizopodia", and various types of "reticulopodia". This is much broader outcome than it was expected during initial studies on foraminiferal morphogenesis. In consequence, it is supposed that an ideal model of cytoskeletal dynamics should simulate all possible states related to feeding activity (reticulopodial networks); motility (single rhizopodia and/or reticulopodia); chamber formation (fan-shaped rhizopodia), aggluti-

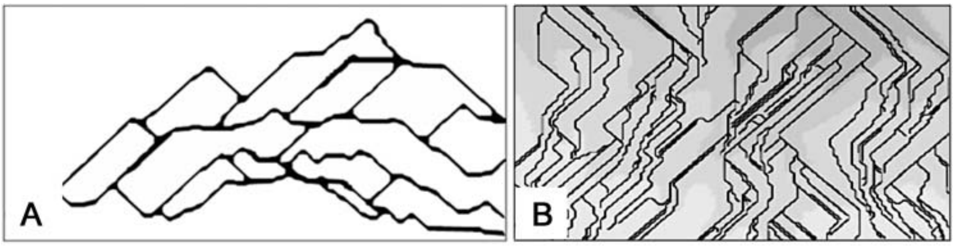

Fig. 7. **A** – Anastomosing network generated by MANGraCA, i.e., Model of Anastomosing Network with Graph of Cellular Automata (from Topa & Paszkowski, 2002, fig. 4c, modified); **B** – Root-like river pattern generated by the similar model; darker shades relate to higher altitudes (from Topa & Dzwinel, 2004, fig. 3f, modified), but may represent gradients of 'morphogens' possibly controlling the growth of rhizopodial networks.

nation of foreign grains (single rhizopodia) etc. This DLA model has presented that all these rhizopodial patterns can be roughly simulated. Nevertheless, our results on simulation of radial (fan-shaped) rhizopodial structures are not convincing because this model cannot mimic regular radial patterns.

Parkinson *et al.* (1999) already modelled much more regular morphogenetic patterns of centric diatoms based on a DLA algorithm. Actually, the reasons of such discrepancies seem to be straightforward because Parkinson *et al.* (1999) used the hexagonal lattice, and our model instead uses the rectangular lattice. This lattice gives less regular, sometimes unexpected results (Fig. 6E–G), which are interesting in themselves, but do not properly mimic the behaviour of radial rhizopodia. In order to improve our results, it is necessary to switch from the rectangular lattice to the hexagonal lattice.

DLA models seem to be very general and narrowly defined parameters only mimic rhizopodial growth. Modelled structures are obviously very sensitive to slight changes in parameters. Another option is to focus on anastomosing networks modelled for anastomosing rivers (Fig. 7; see Topa & Paszkowski, 2002; Topa & Dzwinel, 2004). Actually, foraminiferal rhizopodia form anastomosing structures generally resembling the network of blood vessels, original and artificial neural networks, electricity transmission systems, WWW etc. Their fundamental function is the redistribution of information through the circulation of particles, nutrients, fluids, energy or "pure information" (such as WWW). Such networks appear to be highly optimised, resistant to defects, and in the case of bio-networks, self-repairing.

Therefore, another approach would be to focus on microtubular selforganization itself. Actually, such a model has already been described and implemented by Nédélec *et al.* (1997, 2003). The model simulates self-organisation of tubulin into dynamic mictotubular filaments and interacting with molecular motors, which are responsible for the transport of other molecules such as other microtubules. Nédélec *et al.* (2003) states that due to the size of these filaments, mechanical forces are essential for the organization of the cytoskeleton. This model is very deep and based on real interactions, therefore, we suppose the most promising way would be a combination of our model with certain concepts of the Nédélec *et al.* (1997, 2003) models.

CONCLUSIONS

Three generations of models: from the (1) fixed reference model, through (2) simple moving reference models, to (3) the proposed emergent models are reviewed (Fig. 1A–I). All these models differ in introducing various approaches. The first two (1 & 2) are based on a geometric approach, but contrast in the selection of fundamentally different reference frames: fixed reference and moving reference systems. The second approach introduces apertures as reference points, which are not arbitrarily defined (Fig. 1D–F). Apertures follow the shortest distance between each other (local minimization). This model has tremendously enlarged the number of possible theoretical foraminiferal shells (Fig. 2). The third approach (3) is also based on the moving reference system, but reference points are not just limited to apertures because all particle attachment sites serve as moving references.

Our initial studies on the emergent modelling of foraminifera have shown that the principle approach of going deeper into morphogenetic selforganization of foraminiferal cell is promising. The presented results (see Figs 4–6) are very preliminary and are still not satisfactory, thus, further investigations are necessary. Our future goal would be to attempt to adjust the DLA model so that the results obtained match more closely with empirical data. Another option would be to integrate our model with models focused on microtubular selforganization itself (see Nédélec *et al.*, 1997, 2003).

Acknowledgments

We are grateful to Dr W. Alda, Prof. W. Dzwinel, Dr P. Heinz, Prof. Ch. Hemleben, Prof. V. Hemleben, Prof. J. Hohheneger, Prof. L. Hottinger, Prof. F. Jorissen, Prof. J. Kitowski, Dr habil. B. Korzeniewski, Prof. V. Mikhalevich, Dr M. Paszkowski, and Dr T. Toyofuku for discussions on prospects of foraminiferal modelling. This research is sponsored by the Ministry of Scientific Research and Information Technology (Grant nr 3 PO4D 048 24). We also wish to thank Dr habil. M. A. Gasiński and Prof. J. Hohenegger for reviews, and Dr M. A. Kaminski for linguistic corrections.

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