# Modeling and Visualization of Biological Structures

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## ABSTRACT

Rapid progress in the modeling of biological structures and simulation of their development has occurred over the last few years. It has been coupled with the visualization of simulation results, which has lead to a better understanding of morphogenesis and given rise to new procedural techniques for realistic image synthesis. This paper characterizes selected models of morphogenesis with a significant visual component.

**KEYWORDS:** developmental models in biology, morphogenesis, simulation and visualization of biological phenomena, realistic image synthesis, reaction-diffusion, diffusion-limited growth, cellular automaton, L-system.

> *How far mathematics will suffice to describe, and physics to explain, the fabric of the body, no man can forsee.*
>
> D'Arcy Thompson, *On Growth and Form* [40]

## INTRODUCTION

In the landmark 1984 paper *Plants, fractals, and formal languages* [37], Smith coined the term *database amplification* to denote the synthesis of complex images from small data sets. A generalization of this notion, called *emergence*, became a central notion of *artificial life*. According to Taylor [39, page 31], emergence is a process in which a collection of interacting units acquires qualitatively new properties that cannot be reduced to a simple superposition of individual contributions.

*Morphogenesis*, or the development of complex forms and patterns found in living organisms, provides many striking examples of emergence. Consequently, its models often display an astonishing contrast between the simplicity of the rules expressing the behavior of individual components, and the intricacy of the resulting developmental processes, patterns, and forms.

*Simulation* plays an essential role in the study of morphogenesis. This was anticipated as early as 1952 by Turing, who wrote [42]:

> The difficulties are such that one cannot hope to have any very embracing *theory* of such processes, beyond the statement of equations. It might be possible, however, to treat a few particular cases in detail with the aid of a digital computer. This method has the advantage that is is not so necessary to make simplifying assumptions as it is when doing a more theoretical type of analysis.

*Visualization* of simulation results facilitates their interpretation, and is used as a method for evaluating models. Lacking a formal measure of what makes two patterns or forms (such as trees) look alike, we rely on visual inspection while comparing the models with the reality. For example, Plate 1 shows a photograph and a model of the shell *Natica enzona*, juxtaposed to facilitate visual evaluation of the model. The natural and synthetic pigmentation patterns differ in details, yet we perceive them as fairly similar. This observation contributes to the plausibility of the model, although it does not constitute its definitive validation.

*Photorealistic presentation* of the models aids in their comparisons with the natural structures, and makes models useful for image synthesis applications, such as computer animation, landscape design, and computer art. For example, Plate 2 shows a rendering of the Pelican's Foot shell (*Aporrhais pespelecani*), generated by a mathematical model of shell shape, and placed in an artificial context that blurs the distinction between biological and architectural forms.

This paper reviews mathematical models of morphogenesis capable of producing realistic images of modeled patterns and forms. Our motivation is to expose the relationships between models that may eventually lead to a better understanding of morphogenesis, and to collect together those suitable for computer imagery purposes. Models that capture biological forms without simulating developmental processes, such

as [3, 46] are not considered. The paper is concluded by a reflection on the role of computer science in the study of biological pattterns and forms.

## FEATURES OF MODELS OF MORPHOGENESIS

Historically, the study of morphogenesis has been approached from two directions. The first one consists of viewing form as a derivative of growth, and was formulated by d'Arcy Thompson [40, page 79]:

> It is obvious that the *form* of an organism is determined by its rate of *growth* in various directions; hence rate of growth deserves to be studied as a necessary preliminary to the theoretical study of form.

The second direction focuses on the flow of substances through a tissue and was initiated by Turing [42, page 38]:

> The systems considered consist of masses of tissues which are *not growing*, but within which certain substances are reacting chemically, and through which they are diffusing. These substances are called *morphogens*, the word being intended to convey the idea of a form producer.

The distinction between these two directions is captured as the first characteristic of the models of morphogenesis on the list given below. This list also includes other features that I have found useful in describing models of biological development from a computer scientist's point of view.

1. Models may be *structure-oriented*, focusing on the components of the developing structure, or *space-oriented*, capturing the whole space that embeds this structure. A model in the first category typically describes *where* each component of the structure is located. A model in the second category describes *what* is located at (or what is the state of) each point of space.

2. The developing *structure* and the *space* that embeds it may be *continuous* or *discrete*. The *state* characterizing each point or cell in space may be chosen from a continuous or discrete domain. The model may operate in continuous or discrete *time*.

3. Models may have different *topologies*, such as a non-branching *filament* (sequence of discrete components, or *modules*), a *branching structure*, a *network* (graph with cycles), a 2D *surface*, or a 3D *solid object*.

4. The model may occupy *constant space* or may *expand* (and contract) over time. In the latter case, the expansion may be limited to the *boundary* of the structure, or may take place in the *interior* as well.

5. The *neighborhood relations* between modules may be *fixed* at the time of their creation (determined by the division pattern of modules), or the modules may be *mobile*. In the continuous case, the developmental processes may be viewed as taking place in an *elastic medium* or in a *fluid*.

6. *Communication* between the modules may have the form of *lineage* (information transfer from the parent module to its offspring) or *interaction* (information transfer between coexisting modules). In the latter case, the information flow may be *endogenous* (between adjacent components of the model) or *exogenous* (through the space embedding the model).

We will now use these characteristics to survey selected models of morphogenesis that include a significant visual component.

## SPACE-ORIENTED MODELS

### Reaction-diffusion pattern models

Reaction-diffusion models were developed by Turing to explain the "breakdown of symmetry and homogeneity," leading to the emergence of patterns in initially homogeneous, continuous media [42]. The patterns result from the interaction between two or more morphogens that diffuse in the medium and enter into chemical reactions with each other. Mathematically, this process is captured by a system of partial differential equations. For properly chosen equations and parameter values the uniform distribution of morphogens is unstable. Random fluctuations are amplified and produce a stable pattern of high and low concentrations, which can be represented using different colors in the final image.

Reaction-diffusion models have been extensively studied in theoretical biology, where they provide plausible explanations of many observed phenomena [17, 25, 28]. Ouyang and Swinney recently validated the basic assumptions of these models by realizing reaction-diffusion processes in chemical experiments [29]. In computer graphics, Turk [43] applied the original Turing equations to generate spot patterns, and a five-morphogen system proposed by Meinhardt [25, Chapter 12] to generate stripe patterns covering three-dimensional models of animals. Fowler *et al.* [8] synthesized realistic images of shells (Plate 1) using the model of pigmentation developed by Meinhardt and Klinger [26]. Witkin and Kass [48] extended the application of reaction-diffusion models to non-organic textures.

Figure 1: A venation pattern generated using Meinhardt's model of net-like structures on a hexagonal grid

Reaction-diffusion models may be also suitable for generating the visually attractive patterns found in butterfly wings and flower petals. Unfortunately, the biological literature focuses on models describing small elements of these patterns, such as an eyespot in a butterfly wing. This is not sufficient in image synthesis applications, where we need to reproduce the appearance of the whole structure.

#### A reaction-diffusion model of differentiation

Meinhardt [24] (see also [25, Chapter 15]) extended reaction-diffusion models to capture differentiation of net-like structures from an undifferentiated medium. Figure 1 shows a venation pattern produced using his model. The reaction-diffusion equations are solved on a hexagonal grid (in this case). The state of each cell is characterized by concentrations of four morphogens, one of which determines whether a cell is in a differentiated state and belongs to the structure, or in a nondifferentiated state and belongs to the medium. The simulation begins with the creation of a filamentous succession of differentiated cells, extending at the growing tip of the filament. During the development the tip may split, creating dichotomous branches. At a sufficient distance from the tip (monitored by decreasing concentration of another morphogen, the inhibitor, produced by the tip), the filament initiates lateral branches. Next-order branches are formed in a similar way, if no growing tips are nearby.

This model combines continuous and discrete components. On the one hand, the morphogens diffuse in a continuous medium. On the other hand, differentiation is described at the level of discrete cells.

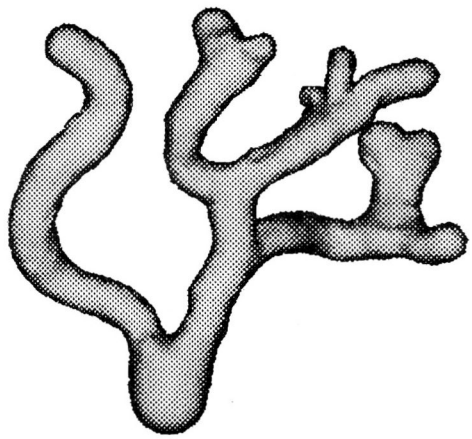

Figure 2: A model of the sponge *Haliclona occulata*, developed by Kaandorp

#### Diffusion-limited accretive growth

In many developmental processes there is an obvious distinction between the structure and the surrounding medium. The focus of the model is then on the gradual expansion of the structure at its border, termed *accretive growth* [20].

Eden [6] simulated the accretive growth of a cell cluster in a square lattice by sequentially adjoining randomly selected cells to the structure formed during previous steps. Meakin [23] (see also [45]) improved this model by assuming that the growth rate (the probability of adjoining a new cell) depends on the local concentration of nutrients that diffuse from a surrounding exterior source and are consumed by the growing structure. Kaandorp [20] applied a three-dimensional variant of this *diffusion-limited growth* process to simulate and visualize the development of corals and sponges. In the first approximation, they expand in the direction of the largest concentration of nutrients (Figure 2). The branching topology is an emerging property of these models, resulting from the higher gradient of nutrient concentration near the tips of the branches than near the origin of the structure.

#### Diffusion-limited aggregation

Witten and Sander proposed a discrete counterpart of diffusion-limited growth, called *diffusion-limited aggregation* (DLA) [49] (see also [45]), which captures diffusion of nutrients by simulating random movement of particles in a grid. The growing structure originates with a single cell. Free particles move in the grid, with the displacement direction chosen at random at each simulation step. Once a moving particle touches the structure formed up to this stage, it sticks to it rigidly.

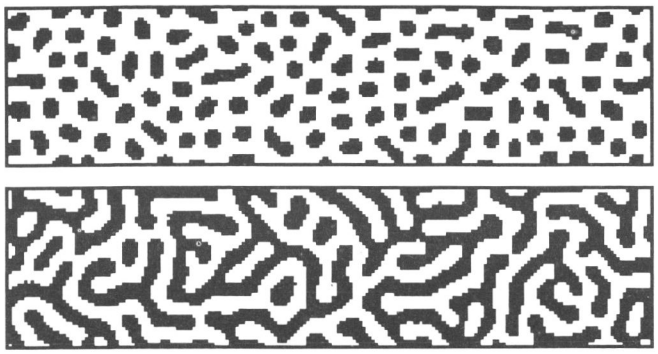

Figure 3: Patterns generated using a discrete counterpart of the reaction-diffusion model, proposed by Young

Diffusion-limited aggregation has attracted considerable research interest, due in part to the fractal character of the emerging branching structures. It is a faithful model of many physical phenomena, such as the deposition of metallic ions on an electrode. It neglects, however, the active role of the organism using nutrients to build its body, and therefore has limited application as a model of growing living structures.

### Cellular automata

*Cellular automata* [41] can be considered a discrete-space counterpart of reaction-diffusion models. The space is represented by a uniform grid, with each site or cell characterized by a state chosen from a finite set. Time advances in discrete steps, and all cells change their states according to the same rule, which describes the next state as a function of the previous state of a cell and its close neighbors.

Young [50] proposed a cellular-automaton model of animal coat patterns using only two cell states: pigmented or not (Figure 3). The resulting patterns are similar to those obtained using continuous reaction-diffusion equations.

In general, the next-state function need not be related to the diffusion of morphogens. Ulam pioneered the application of cellular automata to the simulation of the development of branching structures [44], where the discrete space provides a medium for detecting *collisions* between branches. Figure 4 shows a pattern he termed *Maltese crosses*. The structure differentiates from a (conceptually infinite) square grid of automata beginning with a single seed cell. In each iteration, the pattern expands to the adjacent cells, unless the resulting branches would collide. Figure 5 illustrates the same principle on a triangular grid. A slice of this pattern contained in a 60° wedge is reminiscent of a tree; as noticed by Stevens [38, pages 127–131], this appearance can be reinforced by modifying branching angles while preserving the topology of the model.

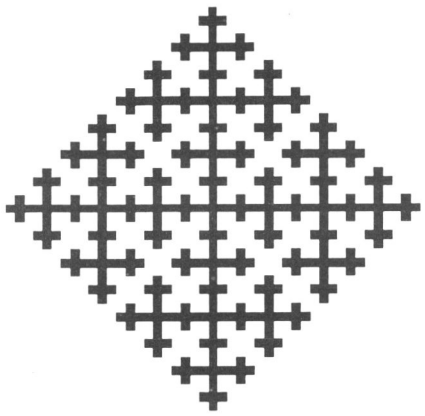

Figure 4: A branching structure generated by Ulam's cellular automaton operating on a square grid

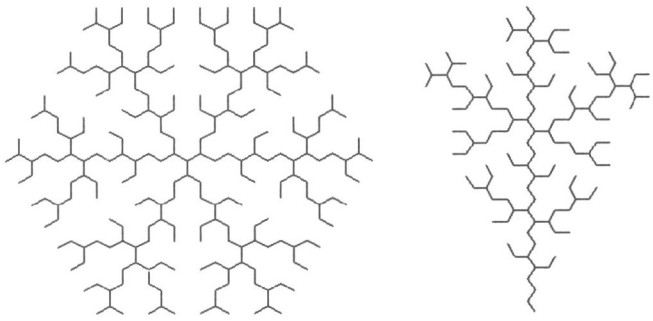

Figure 5: Branching structures generated by Ulam's cellular automaton operating on a triangular grid. Lines connect the centers of cells occupied by the growing structure.

### Voxel automata

Three-dimensional extensions of cellular automata, called *voxel automata* [13], have been used in computer graphics to model aspects of plant development strongly affected by the environment. Arvo and Kirk [2], and Greene [12] applied them to simulate the growth of climbing plants, attaching themselves to predefined objects in space. Subsequently, Greene [13] extended this technique to capture variations in the diameter of branches and roots of a tree, and applied it to simulate the growth of roots searching their path through rocks in the ground, as shown in Figure 6. In this case, the voxels do not represent elements of the structure on the "all or nothing" basis, but hold information about the run of the individual strands that compose branches and roots of the tree. This information is used to keep groups of strands together and guide their development between obstacles in the environment.

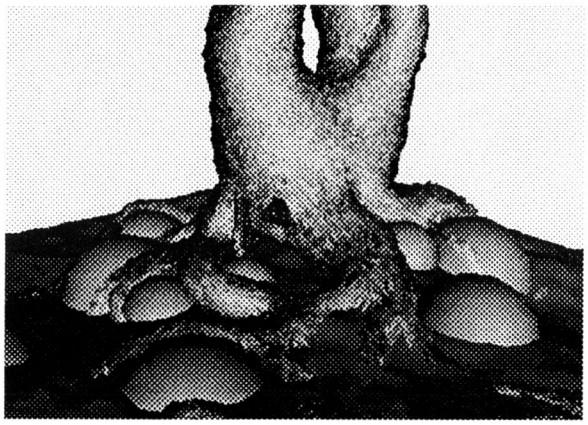

Figure 6: A model of a tree trunk with roots, developed by Greene

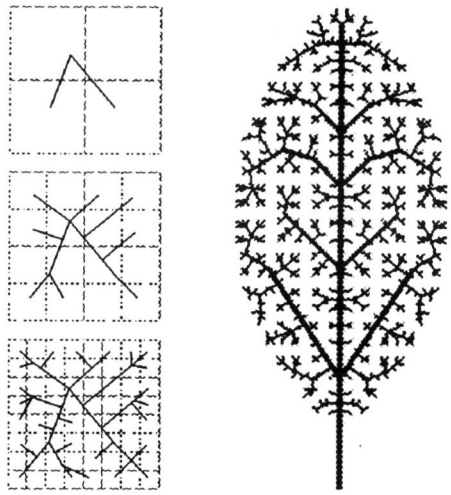

Figure 7: Principle of Gottlieb's method for pattern generation, and a venation pattern modeled using this method

#### Development in expanding space

The models discussed so far can grow only on their boundary. The rigidity of the underlying space, whether continuous or discrete, prevents growth in the interior. Gottlieb [11] proposed a geometric model of development, in which the space expands uniformly. A predefined starting structure is placed in a small square grid (for example, consisting of $2 \times 2$ cells). New branches are created by connecting the centers of grid cells to the structure, provided that the Euclidean distance between a particular center point and the structure exceeds a given threshold. The structure and the cellular space are then scaled twofold, the cells are subdivided, and connections to the centers of the new cells are made in the same way. This process is equivalent to the subdivision of the grid, combined with the reduction of the threshold distance. The above construction is repeated until the desired level of detail is reached, as shown in the left side of Figure 7. The right side of this figure shows the result of applying Gottlieb's method to model leaf venation. This application has a clear biological justification: as a leaf grows, its vascular system is developing in order to maintain the capacity for translocating water, nutrients and products of photosynthesis to and from all parts of the blade. The model exhibits a hierarchical organization of the veins, but there is still a discrepancy between their layout and patterns observed in nature. Faithful modeling of leaf venation remains an open problem.

### STRUCTURE-ORIENTED MODELS

In contrast to space-oriented models, which describe the entire space including the modeled structure, structure-oriented models focus on the development of components that constitute the structure.

#### L-systems

*L-systems* simulate the development of linear and branching structures built from discrete modules [21]. The development can be controlled by lineage (in context-free, or 0L-systems) and by endogenous interaction (in context-sensitive, or IL-systems). The modules represent individual cells of simple multicellular organisms, or larger modules of higher plants (for example, such a internodes, apices, leaves, and branches). L-systems were originally limited to the specification of the topology of branching structures, but subsequent geometric interpretations have made it possible to visualize simulation results [33, 32]. For example, Plate 3 shows a simulated development of the herbaceous plant *Mycelis muralis*.

Although L-systems were introduced as a purely discrete model, practical applications revealed the need for shifting their various aspects to the continuous domain. *Parametric L-systems* [32] have made it possible to express concentrations of substances propagating in the modeled structure. *Differential L-systems* extended L-systems to the continuous time domain, facilitating computer animation of developmental processes [30].

L-system can capture changes of shape that take place during development. The modeled structures may expand at the extremities (subapical growth) as well as in the internal parts (elongation of internodes). Unfortunately, the changes of the relative positions of modules make it difficult to incorporate exogenous control mechanisms, which rely on information flow through the space embedding the model. Prelimi-

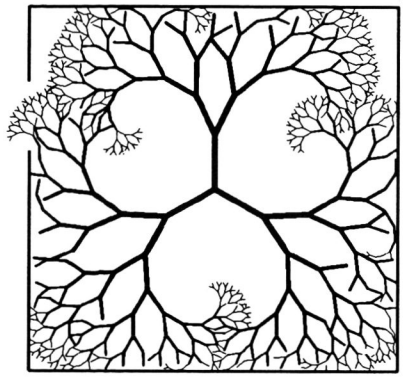

Figure 8: Development of a branching structure, confined to a square box with an incomplete edge. This model was generated using an "environmentally sensitive" L-system inspired by Kaandorp [19].

nary results include detection of collisions between branches themselves and between branches and the environment (Figure 8), and the removal of leaves shaded by other leaves and branches.

Although this example demonstrates the possibility of incorporating exogenous control mechanisms into models expressed using L-systems, many practical problems remain open. For example, the existing "environmentally-sensitive" extensions of L-systems are not specified within the framework of an L-system-based modeling language [16, 31] and require the incorporation of model-specific software modules into the simulation program.

L-systems are related to several other plant models. As shown in [32, Chapter 2], parametric L-systems can reproduce the tree models developed by Aono and Kunii [1], which in turn were based on models by Honda [18]. Françon [10] observed that L-systems can also capture the models of tree architecture classified by Hallé *et al.* [15], and the AMAP models originated by de Reffye [5]. Stochastic L-systems can emulate grass models described in terms of particle systems by Reeves and Blau [34] (Plate 4). Further analysis is needed to establish detailed relationships between these classes.

### Map L-systems

*Map L-systems* [22] extend the expressive power of L-systems beyond branching structures to graphs with cycles, called *maps*, representing cellular layers. Their geometrical interpretation is more difficult than that of branching structures, because the presence of cycles makes it impossible to assign metric properties to the model using local rules. For example, the angles between the edges of a quadrilateral cycle must sum to 360°, and therefore cannot be specified independently from each other. Fracchia *et al.* [9] (see also [32, Chapter 7]) proposed a physically-based solution to this problem. The cells are assumed to have physical properties, osmotic pressure and wall tension, and form a final configuration by mechanically pushing each other until an equilibrium is reached.

Map L-systems have been successfully applied to model fern gametophytes [4, 32]. For example, Plate 5 compares a microphotograph and a computer generated image of the fern thallus *Microsorium linguaeforme*. The natural and the simulated shapes look alike, which supports the hypothesis that the timing and orientation of cell divisions are the dominant factors determining the global thallus shape.

Map L-systems with geometric interpretation operate by first establishing the neighborhood relations between the cells, then assigning geometric parameters to the resulting graph. This approach is biologically justified in multicellular plant structures, since plant cells are tightly cemented together, but is inappropriate in models of animal tissues, since animal cells can move with respect to each other. A model of morphogenesis addressing this problem is described next.

### Mobile cells in a continuous medium

Fleischer and Barr [7] proposed an extensible simulation framework for studying morphogenesis that focused on the generation of connectivity patterns during neural development. Their model consists of discrete cells embedded in a continuous substrate. The actions of the cells are divided into continuous processes (grow, move) and discrete events (divide, create a dendrite, die). The cells move in response to physical forces and interact with other cells and the substrate through mechanical, chemical, and electrical means. Internally, the activity of each cell is governed by a set of conditional differential equations that depend on the cell's state and the local environment. These equations represent the "genetic information" of the cell and describe the changes to an array of variables controlling cell's behavior (movements, growth, divisions). The substrate acts as a medium in which chemical substances diffuse, dissipate, and enter into reactions. A sample frame from a simulation carried out in this environment is shown in Plate 6. The yellow cells appear first, then some of them differentiate into blue cells. The blue cells grow and gradually form a connected skeleton.

Map L-systems and the Fleischer-Barr model present opposite approaches to the definition of multicellular structures. In map L-systems, grammar-based rules specify a model's topology, which subsequently determines its geometry. The cells cannot move with respect to each other. On the other hand, in the FB-model cell movements determine their relative positions; the resulting clusters of adjacent cells indi-

rectly specify topological properties of the emerging structure. The work of Mjolsness *et al.* [27] presents a step towards a synthesis of both approaches: a model in which spatial relationships between the cells *and* grammar-based productions can be combined to specify dynamic changes in system configuration.

Although the FB-model is directed at the study of morphogenesis, it may also provide a unifying framework for considering other phenomena in which autonomous agents move in space and interact. In the computer graphics context, these include behavioral animation, exemplified by Reynolds' model of flocks, herds, and schools [35], and Wejchert and Haumann's model of leaves flying in the air [47].

## CONCLUSIONS

We have surveyed and characterized selected visual models of morphogenesis suitable for image synthesis purposes. The models were divided into two main classes, space-oriented and structure-oriented. We have shown that the space-oriented models capture the flow of information in the medium, but usually have only limited capability to describe expansion of the medium and of the structure embedded in it: growth is limited to the boundary. The structure-oriented models, on the other hand, can simulate the expansion of the whole structure, but often do not capture the information flow through the medium. The selection of the appropriate paradigm is an inherent part of modeling a given phenomenon, as described by Segel [36, page xi],

> A good mathematical model — though distorted and hence "wrong", like any simplified representation of reality — will reveal some essential components of complex phenomenon. The process of modeling makes one concentrate on separating the essential from the inessential.

In same cases, similar patterns or developmental sequences can be generated by fundamentally different models. For example, the *Maltese crosses* shown in Figure 4 were generated using a cellular automaton that explicitly detected and eliminated collisions between branches, but exactly the same pattern can be generated using a context-free L-system. The pigmentation pattern of an *Oliva* shell shown in Figure 9 was generated using a reaction-diffusion model, but similar patterns can be generated using cellular automata and context-sensitive L-systems. Lindenmayer proposed to address such equivalences in a formal way [21]:

> In view of the large number of possible models which give rise to similar morphogenetic patterns, the most important problem is that of narrowing down the set of possibilities. This can be ultimately done on the basis of experimental evidence only. But a better theoretical understanding of equivalence relationships among models of different types would help considerably to sharpen the questions asked in the experiments.

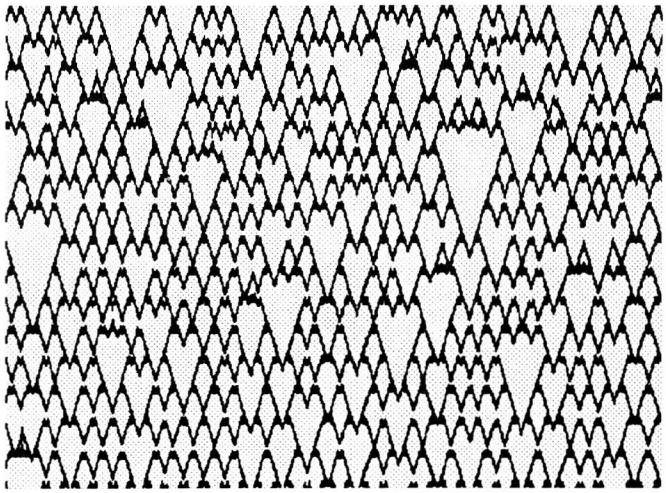

Figure 9: Pigmentation pattern of *Oliva porphyria*, generated using a reaction-diffusion model proposed by Meinhardt and Klinger [26].

A formal theory of pattern complexity would be an important step in this direction. Traditional measures of complexity, such as the time and space needed by a Turing machine to execute an algorithm, fail to quantify the flow of information between components of a developing pattern or structure. A more specialized theory is therefore needed to formally evaluate the alternatives, and provide measurable criteria for selecting the most plausible model of an observed phenomenon. An interesting feature of this methodology is that computer science is being applied to study processes taking place in nature. Gruska and Jürgensen comment [14]:

> "Computer science" should be considered as a science with aims similar to those of physics. The information processing world is as rich and as important as the physical world for mankind.

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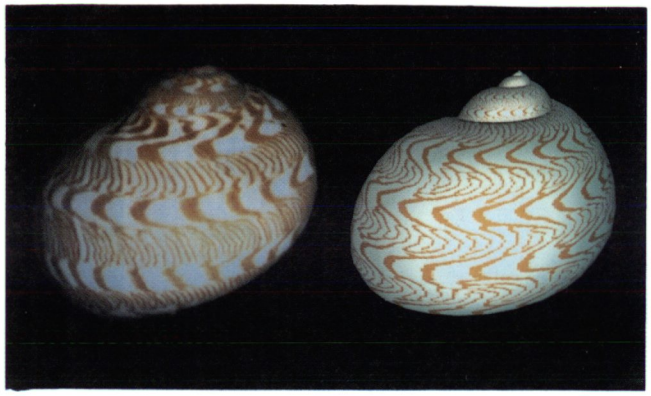

Plate 1: A photograph and a model of *Natica enzona* (Fowler, Meinhardt, Prusinkiewicz, 1992)

Plate 2: *Pelican beach* (Fowler, Prusinkiewicz, 1993)

Plate 3: Developmental model of *Mycelis muralis* (Prusinkiewicz, Hanan, 1987)


Plate 4: *Summer grass* (Orth, 1993)

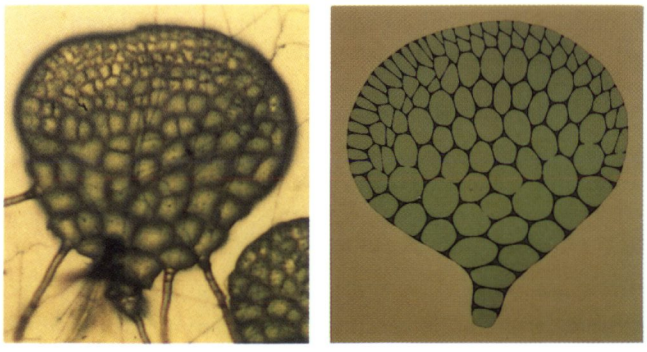

Plate 5: A photograph and a model of *Microsorium linguaeforme* (Fracchia, Prusinkiewicz, de Boer, 1990)

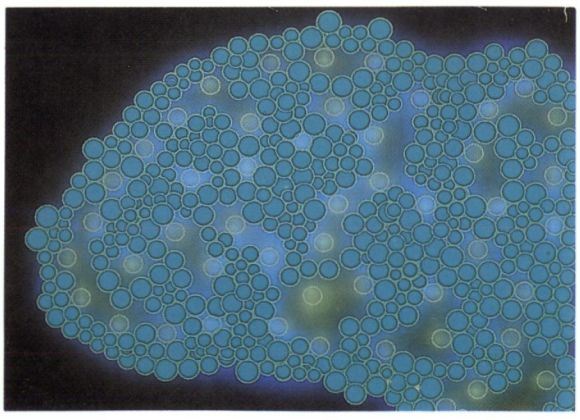

Plate 6: Simulation of mobile cells interacting in a continuous medium (Fleischer, Barr, 1993)