A model for cellular development in morphogenetic fields

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Abstract: This paper introduces *cell systems* as a new framework for the simulation of pattern and shape formation in two-dimensional cellular structures. Cell systems describe development in terms of lineage rules, with the orientations of division walls specified relative to a directional morphogenetic field. The shapes of cells result from mechanical cell interactions due to osmotic pressure and wall tension. Cell systems offer a highly intuitive method for describing the development of cellular structures, and capture their natural variability in a straightforward way. The concept is illustrated using abstract patterns and a developmental model of a fern gametophyte.

Keywords: developmental models in biology, computer simulation, cell system, map L-system, cell division pattern, morphogenetic field, fern gametophyte

1 Introduction

An important issue in developmental biology is the exploration of *morphogenesis*, or mechanisms responsible for the development of complex forms found in living organisms. Cellular structures in plants are determined by the underlying *cell division patterns*, that is, the spatial and temporal distributions of cell divisions. Their analysis reveals the recursive nature of many cell lineages [15].

Map L-systems were proposed by Lindenmayer and Rozenberg [14] as a formal description of developmental sequences of cell patterns. They operate on graphs with cycles, called *maps* [19], with regions representing cells, and edges representing cell walls. The topology of a generated structure is determined by production rules operating on the walls. The cells may grow, pushing their neighbors until an equilibrium state is reached [5, 8, 18]. This allows for the investigation of the relationship between the cell division pattern and the overall shape of the structure [4]. Unfortunately, since observations usually capture the behavior of cells rather than walls, they must be translated to wall productions using a laborious, nonintuitive procedure.

In order to describe the development of fern gametophytes in a more straightforward way, de Boer and de Does introduced the notion of *cell division systems* [4]. They employ two types of rewriting rules,

$$A \rightarrow \frac{B}{C} \qquad \text{and} \qquad A \rightarrow B \mid C,$$

to represent the division of cell A into daughter cells B and C. The horizontal and vertical bars indicate the approximate orientation of the division wall, which can be parallel (*periclinal*) or perpendicular (*anticlinal*) to the closest section of the apical front of the thallus. Cell division systems specify patterns at a sufficient level of detail for growth analysis, but abstract from the precise positions of division walls needed to simulate development.

This paper introduces *cell systems* as a new framework for the simulation of pattern and shape formation in two-dimensional structures. They can be viewed as an extension and a formalization of cell division systems, allowing for a precise specification of the orientation of division walls. This is accomplished by referring to a *vector field*, regarded as a *morphogenetic field* that provides directional information to the cells. Vector fields may be specified independently of the structure or be controlled locally by the structure itself. Examples include light direction, gravity, and concentration gradient of a morphogen. As in map L-systems, the geometry of the generated structures is determined by the mechanical interaction of cells due to cell pressure and wall tension.

This paper focuses on the general concept of context-free cell systems, while leaving the detailed characterization and mathematical analysis for future study. Section 2 provides the definition of cell systems, introduces a notation for rule specification, and presents simple examples that explain their operation. As some cell systems are equivalent to known map L-systems, the natural question of the relationship between both formalisms is addressed in Section 3. Section 4 presents the construction of a cell system for the development of the fern gametophyte *Microsorium linguaeforme*. Finally, Section 5 evaluates the inherent properties of cell systems from a biological perspective, and proposes future extensions.

2 Context-free cell systems

This section formalizes the notion of cell systems as rewriting systems operating on cellular structures.

Definition 2.1. A *cellular structure* is a finite set of cells, each characterized by its *shape* and *state*. The cells are bounded, simple, non-overlapping polygons that tile a surface, thus forming a *polygon mesh* [7, page 473].

The discussion is limited to two-dimensional *cellular layers*, in which cells are characterized by their outlines, as seen under a microscope. The shapes of cells result from the action of mechanical forces: internal cell pressure and tension of cell walls. In multicellular structures, neighboring cells exercise pressure on both sides of the shared walls, thus pushing each other until a global equilibrium is reached. Details of this model are given below.

Definition 2.2. The *pressure-tension model* of physical cell structure consists of the following postulates:

- the modeled structure is represented as a single layer of cells,
- the layer is represented as a two-dimensional network of masses, corresponding to cell vertices, connected by springs that correspond to cell walls,

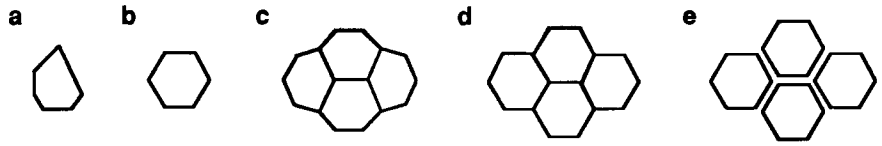

Figure 1: The operation of the pressure-tension model. Description in text.

- the springs are always straight and obey Hooke's law, $F = -k(x - x_0)$,
- each cell exerts pressure on its bounding walls directly proportional to the wall length and inversely proportional to the cell area,
- the pressure on a wall is divided evenly between its vertices,
- the motion of the masses is damped, and
- no other forces (for example, due to friction or gravity) are considered.

The shape of a structure defined using the pressure-tension model can be found by integrating the equations of motion of the masses [8, 18].

Example 2.1. Figure 1 illustrates the operation of the pressure-tension model. The shape (b) results from the initial shape (a), provided that all rest lengths x_0 and all spring constants k are equal. Identical springs are also assumed in structure (c), while (d) has internal walls two times stronger than the external walls, $k_i = 2k_e$. The latter case can be conceptualized as a juxtaposition of separate cells (e), with pairs of adjacent walls fused into single walls. This interpretation explains the regular shape of cells in (d).

Cell division is the engine of the development of cellular structures. The positions of the division walls are specified using the assumption that the development takes place in a vector field.

Definition 2.3. A vector field $\mathcal{Z}$ over a surface X is an assignment of a vector $\vec{Z}$ to each point of X.

Sample vector fields are shown in Figure 2. In the case of a uniform field (a), the reference vectors $\vec{Z}$ point in the same direction for all points in the field. Case (b) is similar, except that the vectors $\vec{Z}$ change direction between the developmental steps. In case (c), the reference vectors indicate the direction towards the closest point on the boundary of the structure, thus the field lines are mutually orthogonal to the family of curves equidistant from the border. In case (d), the reference vectors are specified during the process of cell division as normal to the division wall for each of the daughter cells. This vector field is frequently used throughout this paper and is referred to as the *polarity vector field.*

A multitude of other fields can be found easily, hence their classification is needed. The fields that do not change over time are referred to as *stationary* (a). The complementary class of *non-stationary* fields contains those that do not depend on the embedded structure (b), those that depend on global properties of the structure (c) and those that depend on its local properties (d). Any non-stationary field can be considered formally as a function

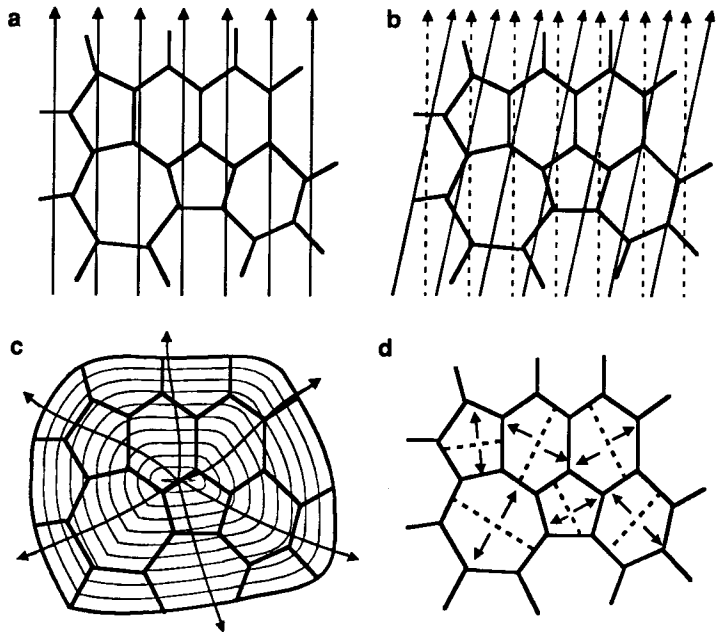

Figure 2: Sample vector fields embedding a cellular structure

of time. However, such a definition may obscure possible explicit dependencies between the model and the field (c and d).

Definition 2.4. A *context-free cell system* $\mathcal{H}$ over a vector field $\mathcal{Z}$ consists of:

- a finite *alphabet* of cell states (types) Σ,
- a *starting cellular structure* ω with cell labels from Σ, and
- a finite *set of cell productions* (developmental rules)

$$P \in (\Sigma \times \Sigma) \cup (\Sigma \times \Sigma \times \Re \times (0,1) \times \Sigma) ,$$

where $\Re$ denotes the set of real numbers. It follows that productions may have two forms. A production $(A, B) \in P$, written $A \longrightarrow B$, changes the cell label from A to B. A production $(A, B, \alpha, r, C) \in P$, written $A \longrightarrow B \uparrow (\alpha, r) C$, splits cell A into two cells labeled B and C. The orientation of the division wall is specified by the angle α between the direction of the reference vector $\vec{Z}$, measured at the center of gravity of A immediately before the division, and the normal vector to the wall. Cell B lies on the side of the wall opposite to the direction of the normal, while C lies on the side pointed to by the normal. The areas of cells B and C are fractions r and $1 - r$ of the area of the mother cell A (Figure 3). In the frequently occurring case where the areas of cells B and C are the same ($r = 0.5$), the notation $A \longrightarrow B \uparrow (\alpha, r) C$ is shortened to $A \longrightarrow B \uparrow (\alpha) C$.

Definition 2.5. A cell system $\mathcal{H}$ operates in a sequence of *derivation steps*, noted $\mu_i \Longrightarrow \mu_{i+1}$, during which the *predecessor structure* μ_i yields the *successor structure* μ_{i+1} for the subsequent values of the index i. Each derivation step consists of three phases:

- A structure μ'_{i+1} is obtained from μ_i by applying productions from P *simultaneously* to all cells in μ_i. The vector field at the time immediately preceding production application is noted $\mathcal{Z}_i$.

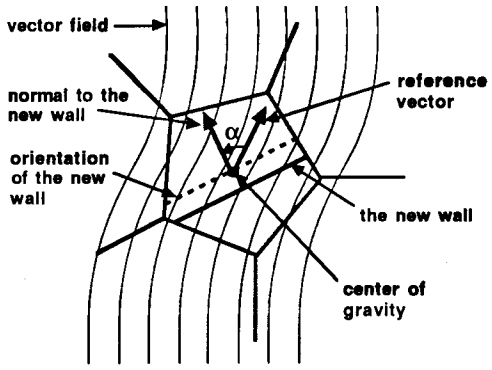

Figure 3: Specification of the division wall with respect to the vector field

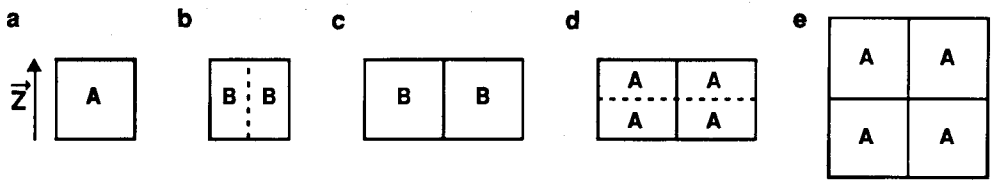

Figure 4: The development of a simple two-dimensional pattern. The original shape (a) undergoes a succession of divisions (b, d), followed by the application of the pressure-tension model (c, e).

- A structure μ_{i+1} is obtained from μ'_{i+1} by applying the pressure-tension model to determine the steady-state geometry of μ_{i+1}. The rest length and the spring constant of the walls, as well as the coefficient relating cell pressure to area, are global parameters of the model.

- The vector field is recomputed (in the non-stationary case), yielding the new field $\mathcal{Z}_{i+1}$, to be used in the subsequent derivation step.

The sequence of structures starting with $\mu_0 = \omega$ is called the *developmental sequence* generated by $\mathcal{H}$.

The above definitions are interpreted as follows. The state of a cell comprehends all features, other than shape, that characterize it at a given moment. At fixed intervals, cells divide or change state without a division. The fate of each cell is determined by the applicable production. If a cell undergoes a division, the production specifies the position of the division wall in addition to the states of the daughter cells. The orientation of the division wall is given by the angle α between the reference vector $\vec{Z}$ and the wall normal. By default, the division wall splits the mother cell into two cells of equal area. Unequal cell division is specified in terms of the relative areas of the daughter cells. After production application, the structure undergoes a period of growth. The resulting geometry is determined by the mechanical interaction between cells. At the end of a derivation step the vector field is updated, providing new reference directions for the subsequent cell divisions. The updating algorithm depends on the modeled structure and is not included in the definition of cell systems.

Example 2.2. Figure 4 shows a simple structure that develops in a uniform stationary field $\mathcal{Z}$, with the vector $\vec{Z}$ pointing up at all points in the field. The alphabet Σ of the

cell system consists of two symbols, A and B. The initial structure ω is a square cell labeled A. The development is governed by two productions that divide cells alternately by vertical and horizontal walls:

$$p_1 : \mathtt{A} \rightarrow \mathtt{B} \uparrow (90)\, \mathtt{B}$$
$$p_2 : \mathtt{B} \rightarrow \mathtt{A} \uparrow (0)\, \mathtt{A}$$

The pressure-tension model operates under the following assumptions:

- the relation between cell area and pressure on the walls is the same for all walls, $pressure = C/area$, where C is a constant,
- the rest length of all walls is equal to 0, and
- the spring constants k_i and k_e for the internal and external walls satisfy the equation $k_i = 2k_e$.

Example 2.3. Figure 5 shows the development of a pattern first studied by Korn and Spalding as an idealized model for cell divisions in the epidermis of onion [10]. According to a subsequent formalization [5, 14], this pattern can be constructed as follows. The initial structure is a single hexagonal cell. During the first derivation step the division wall splits two opposite walls at 1/3 and 2/3 of their length (a). Simple trigonometry shows that the normal to the division wall is at an angle $\alpha \approx -80.89°$ with respect to the reference vector $\vec{Z}$. In subsequent steps, the cells divide in a similar manner, except that the reference direction is defined locally as being perpendicular to the previous division wall (thus, the polarity vector field is used). It is convenient to assume that, from the topological point of view, cell divisions take place on the surface of a torus, thus all walls are shared by two cells (b). Consequently, at each stage of development, the structure consists entirely of hexagons, which are made regular by the application of the pressure-tension model (c).

According to the above description, the Korn-Spalding pattern can be captured by a cell system with a single production,

$$p : \mathtt{A} \rightarrow \mathtt{A} \uparrow (-80.89)\, \mathtt{A}\,.$$

Initially, the field $\mathcal{Z}$ consists of diagonal vectors $\vec{Z}$ (Figure 5a). Subsequently, the reference vectors are specified for pairs of sister cells as normal to the division wall (polarity vector field – Figure 2d).

For the purpose of comparison, Figure 6 shows two patterns obtained by the same cell system operating in the plane rather than on a torus. The border cells usually have less than six walls. This affects divisions of the internal cells, and breaks the regularity of the original pattern.

Example 2.4. Figure 7 shows a slightly more complex pattern composed of cells with five, six, and seven walls [2]. The corresponding cell system is given below.

$$\omega : 5$$
$$p_1 : 5 \rightarrow 6 \uparrow (-95.5, 0.67)\, 5$$
$$p_2 : 6 \rightarrow 7 \uparrow (-109.0, 0.78)\, 5$$
$$p_3 : 7 \rightarrow 7 \uparrow (-93.5, 0.67)\, 6$$

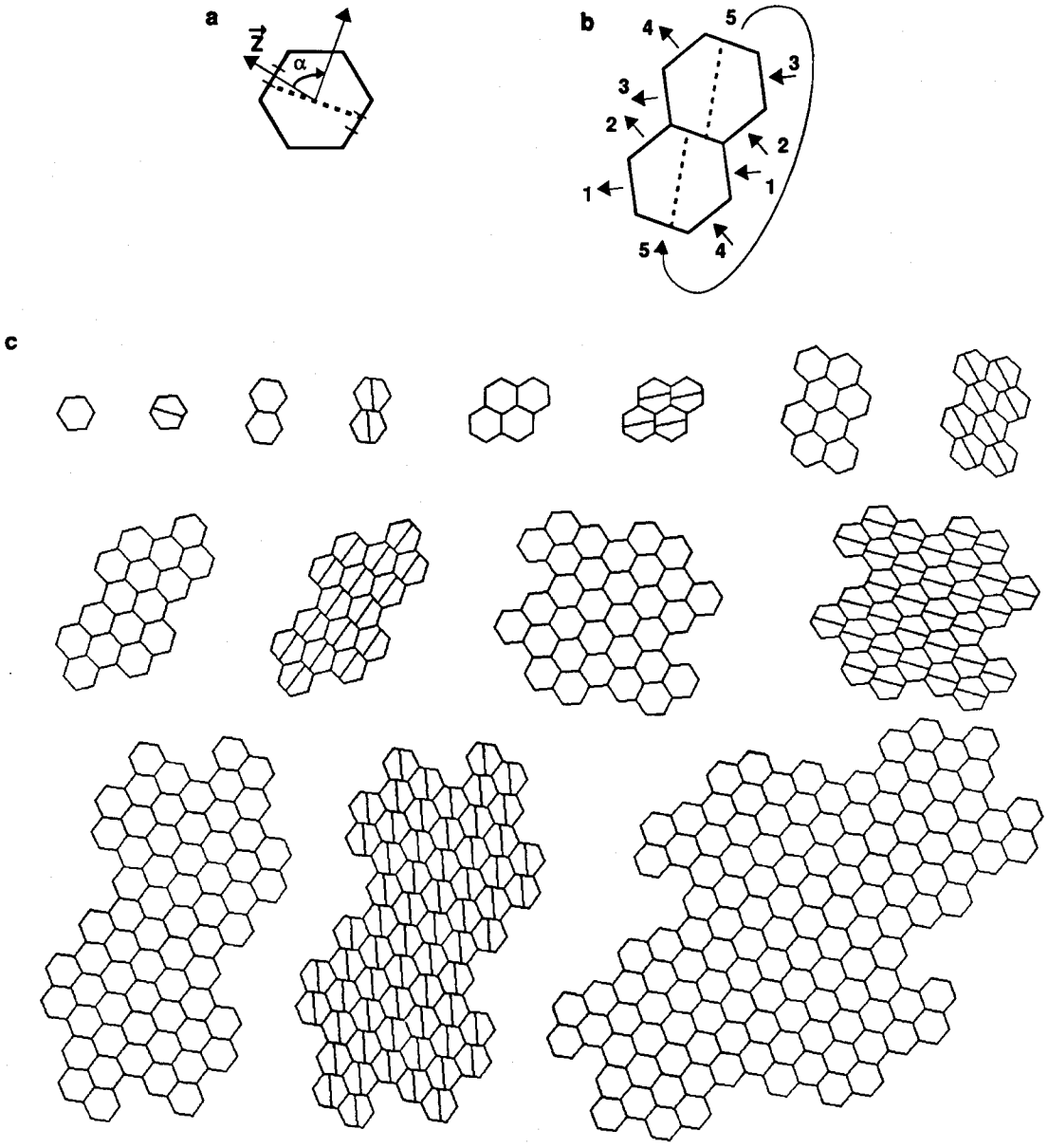

Figure 5: Construction of the *Korn-Spalding* pattern. (a) Geometry of wall insertion. (b) Neighborhood relations between walls on the surface of a torus. Arrows indicate pairs of walls 'fused' together. (c) The developmental sequence.

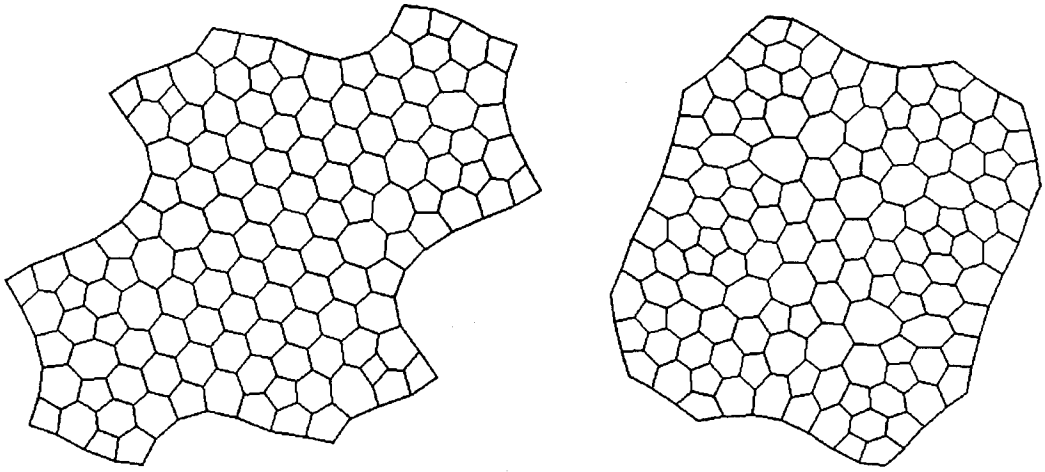

Figure 6: Derivatives of the Korn-Spalding pattern generated in the plane. (a) The spring constants for the interior and exterior walls are not equal, $k_i = 2k_e$. (b) The spring constants for all walls are equal.

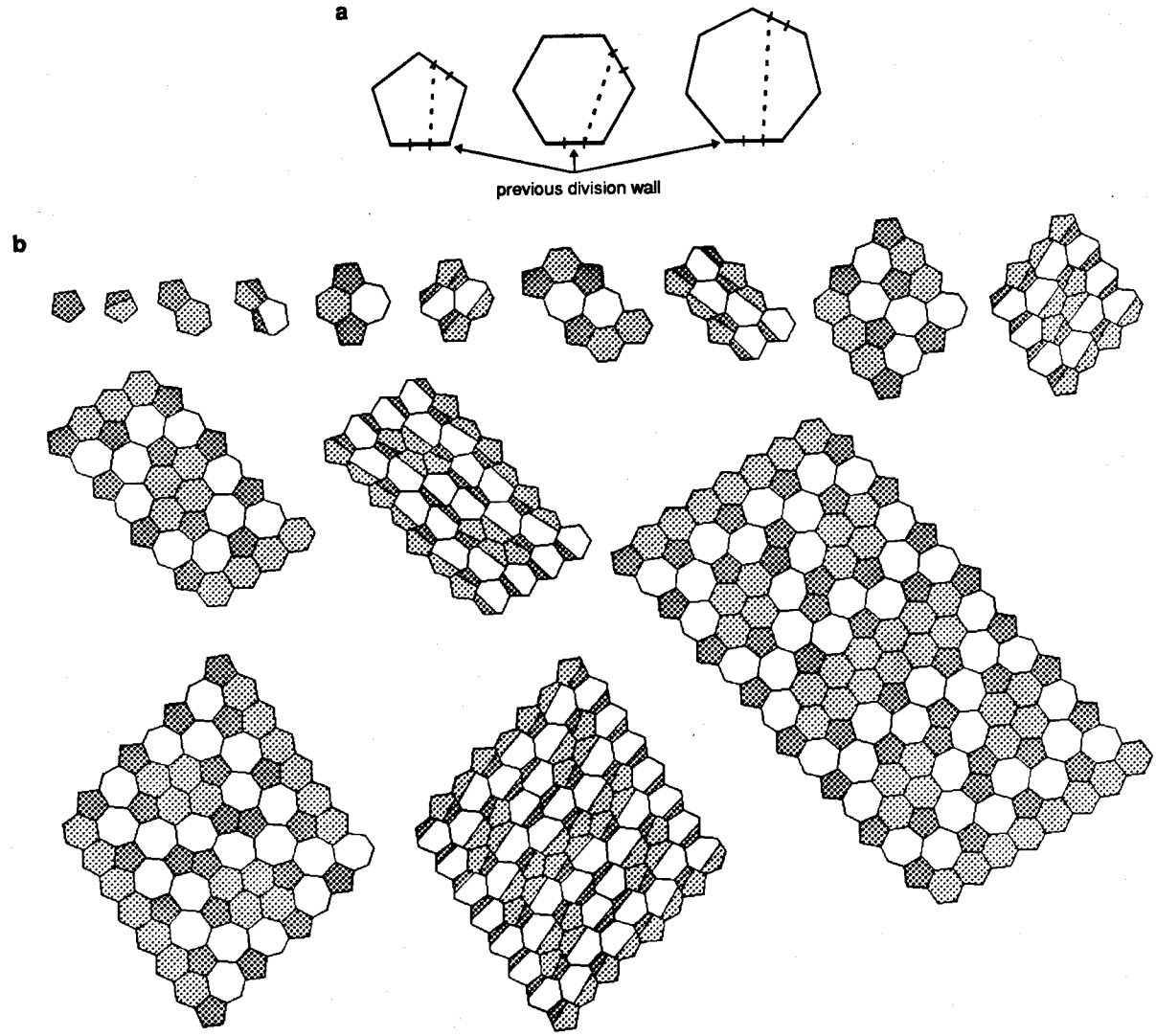

Figure 7: A pattern consisting of cells with five, six, and seven walls. (a) Postulated positions of division walls. (b) The developmental sequence.

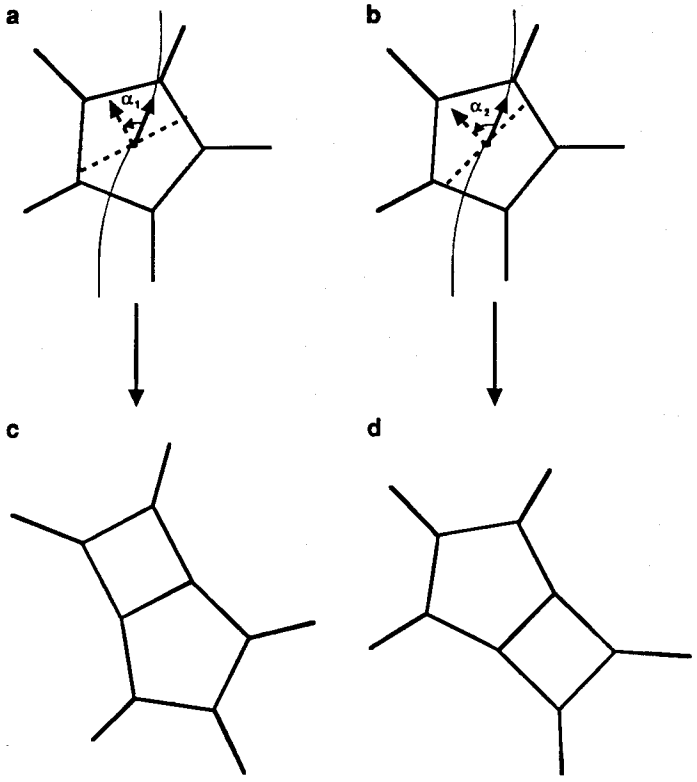

Figure 8: The interlacing of topology and geometry in cell system operation. The angle α determines structure topology after the division wall has been inserted (a,b). The new topology determines geometry at equilibrium (c,d).

The orientation and positions of the division walls were estimated using Figure 7a. As in the case of the Korn-Spalding pattern, the reference direction is the polarity vector field, and the development takes place on a torus.

The structures presented in the above examples can be also generated using map L-systems. It is therefore interesting to compare these two formalisms.

Both map L-systems and cell systems are parallel rewriting systems. Cell systems can be viewed as an extension of string L-systems [12] to polygon meshes, while map L-systems extend string L-systems to maps. The fundamental difference is that a map is a purely topological notion, while a mesh combines topological and geometric aspects (Figure 8). Positions of the inserted walls are specified in geometric terms, yet they determine the topology of the mesh after each step of rule application. The new topology determines, in turn, the geometry of the cellular structure, reached at equilibrium.

The definition of the vector field is a key component of cell system specification and has a paramount impact on its properties. The next section shows that, for the polarity vector field, the generative powers of cell systems and map L-systems are closely related.

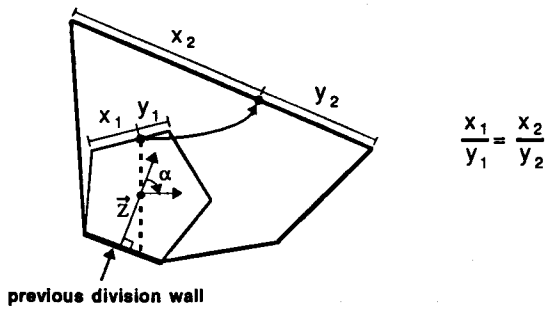

Figure 9: Cell division with regularization.

3 A comparison of cell systems to map L-systems

Strictly speaking, map L-systems and cell systems cannot be compared, since they operate on two different types of objects: maps, which are defined in topological terms, and cellular structures, defined in geometric terms. Nevertheless, it is possible to abstract from the geometry of cells, and view each cellular structure as a representation of a map. Then the classes of maps generated by map L-systems and cell systems can be compared. The following discussion employs binary propagating context-free map L-systems with markers (mBPMOL-systems) [17] as the representative type of map L-systems.

A production in a map L-system can subdivide an existing wall by the insertion of vertices, without attaching a new wall to them. Consequently, a map L-system can introduce vertices of order two into the generated map. In contrast, a cell system creates vertices as attachment points for new division walls, and can only generate vertices of order three or higher. In view of this discrepancy, maps that differ only by the number and the placement of order-two vertices are considered equivalent.

In order to abstract from cell geometry, it is assumed that, prior to division, each cell is transformed into a regular polygon irrespective of other cells (Figure 9). In this process, the previous division wall preserves its position with respect to the vector field. Once a new division wall is inserted, the cell is transformed back to its original shape. This inverse transformation preserves proportions at which two previously existing walls are split by the attachment points of the new division wall. As a result, all cells with the same label are divided in the same way, regardless of shape, as long as they have the same orientation with respect to the vector field $\mathcal{Z}$.

Theorem. Consider a map L-system $\mathcal{G}$ that generates a sequence of maps $\omega_{\mathcal{G}}, M_1, M_2, \ldots$, and assume that all regions have a number of walls bounded by a constant N. It is then possible to construct a context-free cell system $\mathcal{H}$ that generates a sequence of equivalent cellular structures $\omega_{\mathcal{H}}, S_1, S_2, \ldots$.

Proof. The construction of cell system $\mathcal{H}$ is straightforward:

1. Consider the map sequence $\omega_{\mathcal{G}}, M_1, M_2, \ldots$. Find the set of distinct circular words w_i that describe possible sequences of wall labels characterizing regions of these maps. Since the number of productions in the map L-system $\mathcal{G}$ is finite, and the number of walls per cell is bounded by a constant, all circular words will appear in the finite sequence of maps $\omega_{\mathcal{G}}, M_1, \ldots, M_n$ for some n.

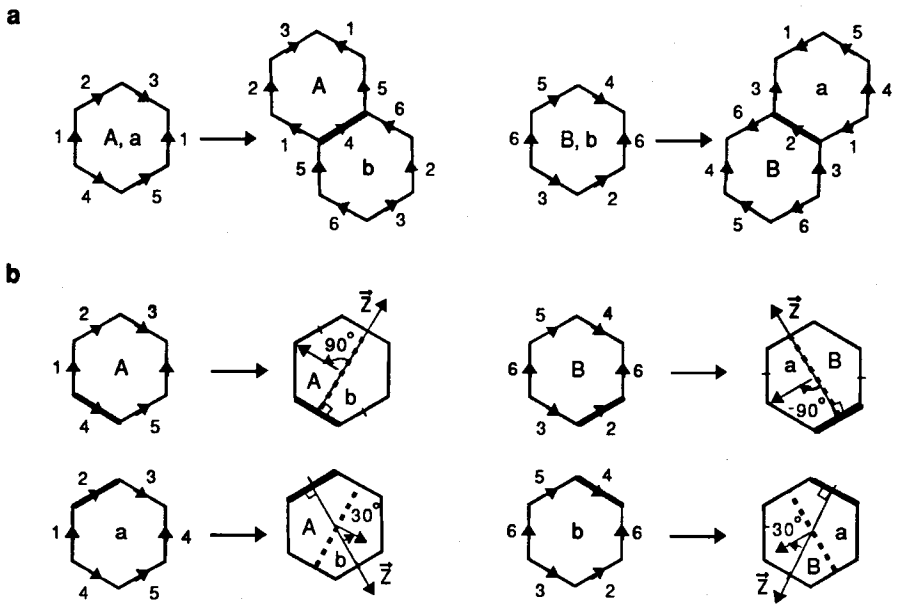

Figure 10: Construction of a cell system from the map L-system for the *Lewis* pattern. (a) Finding the circular words and mapping them to cell labels. (b) Determining the angle between the reference vector and division wall normal for each cell.

2. For each circular word w_i, find the set of marked words $\underline{w}_{ij}$, where the marker indicates the position of the previous division wall. Clearly, the same circular word may result from the partition of various regions, which is why it may admit different markings. If a word occurs only in the initial map $\omega_{\mathcal{G}}$, choose its marking arbitrarily. Since all possible circular words appear in maps $\omega_{\mathcal{G}}, M_1, \ldots, M_n$, the complete set of their successors, and therefore marked words, can be identified in maps $\omega_{\mathcal{G}}, M_1, \ldots, M_{n+1}$.

3. Assign a unique cell label to each marked circular word, and determine the cell production associated with each word using maps $\omega_{\mathcal{G}}, M_1, \ldots, M_{n+1}$. Use the polarity vector field $\mathcal{Z}$ and assume that the cells are regularized prior to division.

4. Transform the initial map $\omega_{\mathcal{G}}$ to the initial cellular structure $\omega_{\mathcal{H}}$ by matching a previously identified marked circular word to each region of $\omega_{\mathcal{G}}$, and assigning the corresponding label to it. The initial structure $\omega_{\mathcal{H}}$ and the cell productions found in Step 3 constitute the cell system $\mathcal{H}$ equivalent to the map L-system $\mathcal{G}$. □

Example 3.1. The following map L-system, specified using notation from [18, pages 146–148], generates the sequence of patterns proposed by Lewis [11] and described formally by Lindenmayer and Rozenberg [14]:

$$
\begin{array}{lll}
\omega: & \overrightarrow{1}\overrightarrow{2}\overrightarrow{3}\overleftarrow{1}\overleftarrow{5}\overleftarrow{4} & \\
p_1: & \overrightarrow{1} \rightarrow & \overrightarrow{2} \\
p_2: & \overrightarrow{2} \rightarrow & \overrightarrow{3}\,[+\,\overrightarrow{2}]\,\overleftarrow{1} \\
p_3: & \overrightarrow{3} \rightarrow & \overleftarrow{5}\,[-\,\overleftarrow{4}]\,\overleftarrow{6} \\
p_4: & \overrightarrow{4} \rightarrow & \overleftarrow{1}\,[+\,\overrightarrow{4}]\,\overleftarrow{5} \\
p_5: & \overrightarrow{5} \rightarrow & \overleftarrow{6}\,[-\,\overleftarrow{2}]\,\overrightarrow{3} \\
p_6: & \overrightarrow{6} \rightarrow & \overrightarrow{4}
\end{array}
$$

Two circular words are generated by this map L-system (Figure 10a): $\overrightarrow{1\,2\,3\,1\,5\,4}$ and $\overrightarrow{6\,5\,4\,6\,2\,3}$.
The production rules for the circular words with underscores indicating the inserted division wall are:

$$\begin{array}{rcl} \overrightarrow{1\,2\,3\,1\,5\,4} & \rightarrow & \overrightarrow{1\,2\,3\,1\,5\,\underline{4}}\ \ \overrightarrow{6\,5\,\underline{4}\,6\,2\,3} \\ \overrightarrow{6\,5\,4\,6\,2\,3} & \rightarrow & \overrightarrow{1\,\underline{2}\,3\,1\,5\,4}\ \ \overrightarrow{6\,5\,4\,6\,\underline{2}\,3} \end{array}$$

The marked circular words can be mapped to cell labels as follows:

$$\begin{array}{rcl} \overrightarrow{1\,2\,3\,1\,5\,\underline{4}} & \mapsto & \mathtt{A} \\ \overrightarrow{1\,\underline{2}\,3\,1\,5\,4} & \mapsto & \mathtt{a} \\ \overrightarrow{6\,5\,\underline{4}\,6\,2\,3} & \mapsto & \mathtt{b} \\ \overrightarrow{6\,5\,4\,6\,\underline{2}\,3} & \mapsto & \mathtt{B} \end{array}$$

The cell system equivalent to the given map L-system has initial structure A and four productions with predecessors A, a, B, and b. The positions of the division walls are found assuming that the structure develops on a torus, thus all cells are regular hexagons (Figure 10b). As stipulated by the proof of the theorem, these positions are expressed with respect to the polarity field vectors.

$$\begin{array}{rcl} \omega: & \mathtt{A} & \\ p_1: & \mathtt{A} & \rightarrow\ \mathtt{b} \uparrow (90)\, \mathtt{A} \\ p_2: & \mathtt{a} & \rightarrow\ \mathtt{A} \uparrow (30)\, \mathtt{b} \\ p_3: & \mathtt{B} & \rightarrow\ \mathtt{B} \uparrow (-90)\, \mathtt{a} \\ p_4: & \mathtt{b} & \rightarrow\ \mathtt{a} \uparrow (-30)\, \mathtt{B} \end{array}$$

The sequence of cellular structures generated by this cell system is shown in Figure 11.

The inverse problem, regarding the existence of an mBPMOL-system equivalent to a given cell system, remains open. As shown in [3], if the cell system generates a sequence of structures with a bounded number of cell walls, it is possible to find an equivalent double-wall map L-system [15, 16]. It can be converted to a map L-system with markers only if the number of configurations of labels on both sides of the walls is finite (the double-wall system has *parity* [3, 15]). At this point it is not clear whether bounded cell systems equivalent to double-wall systems without parity exist.

4 A model of a fern gametophyte

This section presents a cell system that simulates the development of a fern gametophyte *Microsorium linguaeforme*. Its developmental sequence had been previously studied and simulated using map L-systems [2, 4, 18]. The modeling process consisted of the following steps:

1. microscopic observations of the development of sample gametophytes,
2. the expression of observations using a cell division system,
3. translation of the cell division system to a map L-system, and

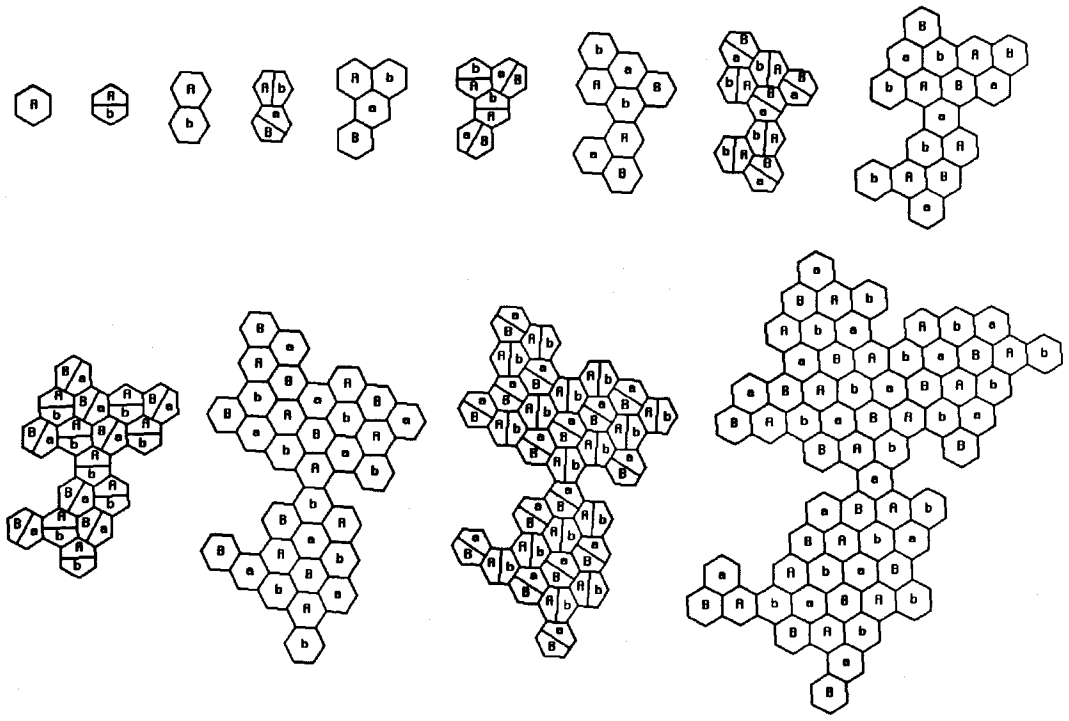

Figure 11: The *Lewis* pattern

4. simulation of the development using this map L-system.

The translation of a cell division system to a map L-system is a laborious process which may introduce rigid assumptions regarding offsets in cell tetrads [15], and yields a nonintuitive description of the modeled structure. We show that a cell system provides a model which captures the observed phenomena in a straightforward way.

A gametophyte of *Microsorium linguaeforme* forms a plant body called a ***thallus*** that is not differentiated into stem, leaf and root. The development of a thallus can be described conveniently in terms of the activity of the *apical cell* and the development of *segments*. The apical cell is the originator of the gametophyte structure. It divides repetitively, giving rise each time to a new apical cell and a primary (initial) segment cell. The division walls are oriented alternately to the left and to the right, yielding two columns of segments separated by a zig-zag dividing line (Figure 12): The recursive nature of the apical activity is captured by the following cell division system.

$$A_L \rightarrow Q_1 \mid A_R \qquad\qquad A_R \rightarrow A_L \mid Q_1$$

The primary segment cells Q_1 subdivide further, yielding multicellular segments. Microscopic observations reveal that most segments follow the same developmental sequence, shown diagrammatically in Figure 13. The cell Q_1 is first divided by a periclinal wall into two cells, Q_2 and Q_3. Subsequently, the cell Q_3 is divided by another periclinal wall into two terminal cells T that do not undergo further divisions. At the same time, the cell Q_2 lying on the thallus border is divided by an anticlinal wall into two cells of type Q_1. Each of these cells divides in the same way as the primary cell. Consequently, the recursive

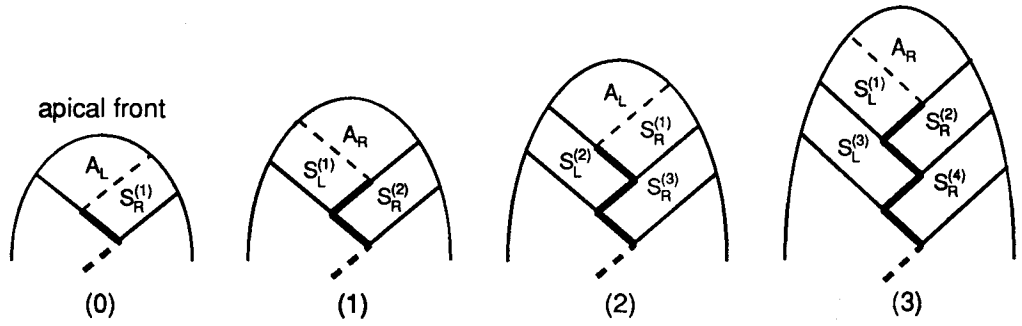

Figure 12: Apical production of segments. The labels A_R and A_L denote apical cells producing right segment S_R and left segment S_L, respectively. Dashed lines indicate the newly created division wall. The superscripts represent segment age. The internal structure of segments is not shown.

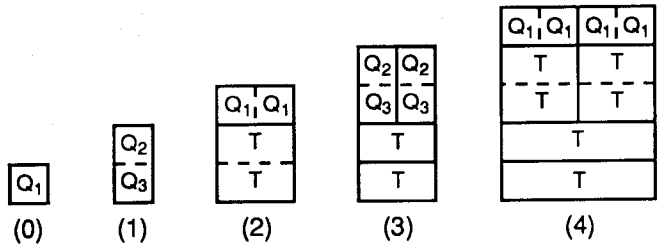

Figure 13: Developmental sequence of a *Microsorium* segment

nature of segment development can be captured by the following cell division system:

$$Q_1 \rightarrow \frac{Q_2}{Q_3} \qquad Q_2 \rightarrow Q_1 \mid Q_1 \qquad Q_3 \rightarrow \frac{T}{T}$$

The two oldest segments, situated at the thallus base, form a modified pattern with less extensive cell divisions. The developmental sequence of the right basal segment is shown in Figure 14. The corresponding cell division system is given below:

$$B_1 \rightarrow \frac{B_2}{T} \qquad B_2 \rightarrow B_1 \mid T$$

The left basal segment follows a symmetric pattern:

$$C_1 \rightarrow \frac{C_2}{T} \qquad C_2 \rightarrow T \mid C_1$$

All of the above productions form a cell division system that captures the recursive pattern of cell divisions in the gametophyte, but lacks precise geometric information needed for simulation. In order to formulate a corresponding cell system, we define a vector field closely related to the organism description in terms of periclinal and anticlinal walls. For any pair of sister cells, the reference vector $\vec{Z}$ is normal to the division wall. In contrast to the polarity vector field of Figure 2d, the vector $\vec{Z}$ has the same orientation in both sister cells. The resulting cell system is given below.

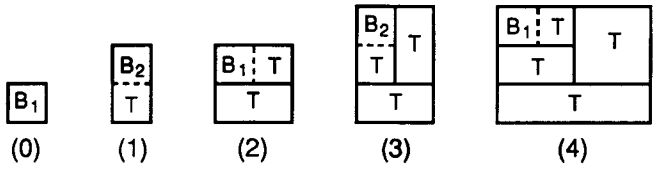

Figure 14: Developmental sequence of the right basal segment

p_1 : $A_L \rightarrow A_R \uparrow (-45.0, 0.3)\, Q_1$
p_2 : $A_R \rightarrow Q_1 \uparrow (45.0, 0.7)\, A_L$
p_3 : $Q_1 \rightarrow Q_2 \uparrow (-98.0)\, Q_3$
p_4 : $Q_2 \rightarrow Q_1 \uparrow (90.0)\, Q_1$
p_5 : $Q_3 \rightarrow T \uparrow (0.0)\, T$
p_6 : $B_1 \rightarrow B_2 \uparrow (-90.0)\, T$
p_7 : $B_2 \rightarrow B_1 \uparrow (90.0)\, T$
p_8 : $C_0 \rightarrow C_1$
p_9 : $C_1 \rightarrow C_2 \uparrow (-90.0)\, T$
p_{10} : $C_2 \rightarrow T \uparrow (90.0)\, C_1$

The cell system closely follows the cell division system with the exception of production p_8, which delays the development of the left basal segment by one step with respect to the right basal segment. The values of angles and relative areas are obtained by comparing simulations to the microscopic observations, and adjusting parameters accordingly. The developmental sequence generated using this cell system is shown in Figure 15. Different gray levels indicate the apical cell, the alternating segments close to the apex, and the pair of basal segments. The model shows good correspondence with the shape of the real organism and with the model expressed using a map L-system [18, page 161]. Although all segments originating from the apical cell develop according to the same cell production rules, they exhibit slightly different division patterns (*segment-to-segment variability*), due to different cell shapes.

The angles at which the division walls are inserted into the mother cells have a pronounced effect on the generated structure. For example, Figure 16 illustrates the result of setting the angles in productions p_1 and p_3 to $-90°$, and p_2 to $90°$. The variability of structures generated using cell systems with different parameters in productions coincides with observations of real gametophyte structures. The ease of capturing *specimen-to-specimen variation* is an asset of cell systems. In contrast, a small change in the developmental sequence simulated using a map L-system may require substantial modifications of many productions.

5 Discussion

This paper presents a new method for the modeling of cell division and expansion in single-layered cellular structures. Cell divisions are described by productions capturing cell lineage. The orientations of the division walls are specified relative to a vector field (morphogenetic field), as opposed to a topological description of the attachment sites. Consequently, cell systems provide a more intuitive description of cell division patterns than map L-systems. The geometry of cells, determined by a model that takes into account internal cell pressure and wall tension, influences the topology of the generated structures. This accounts for a variability in cell division patterns, consistent with that observed in nature.

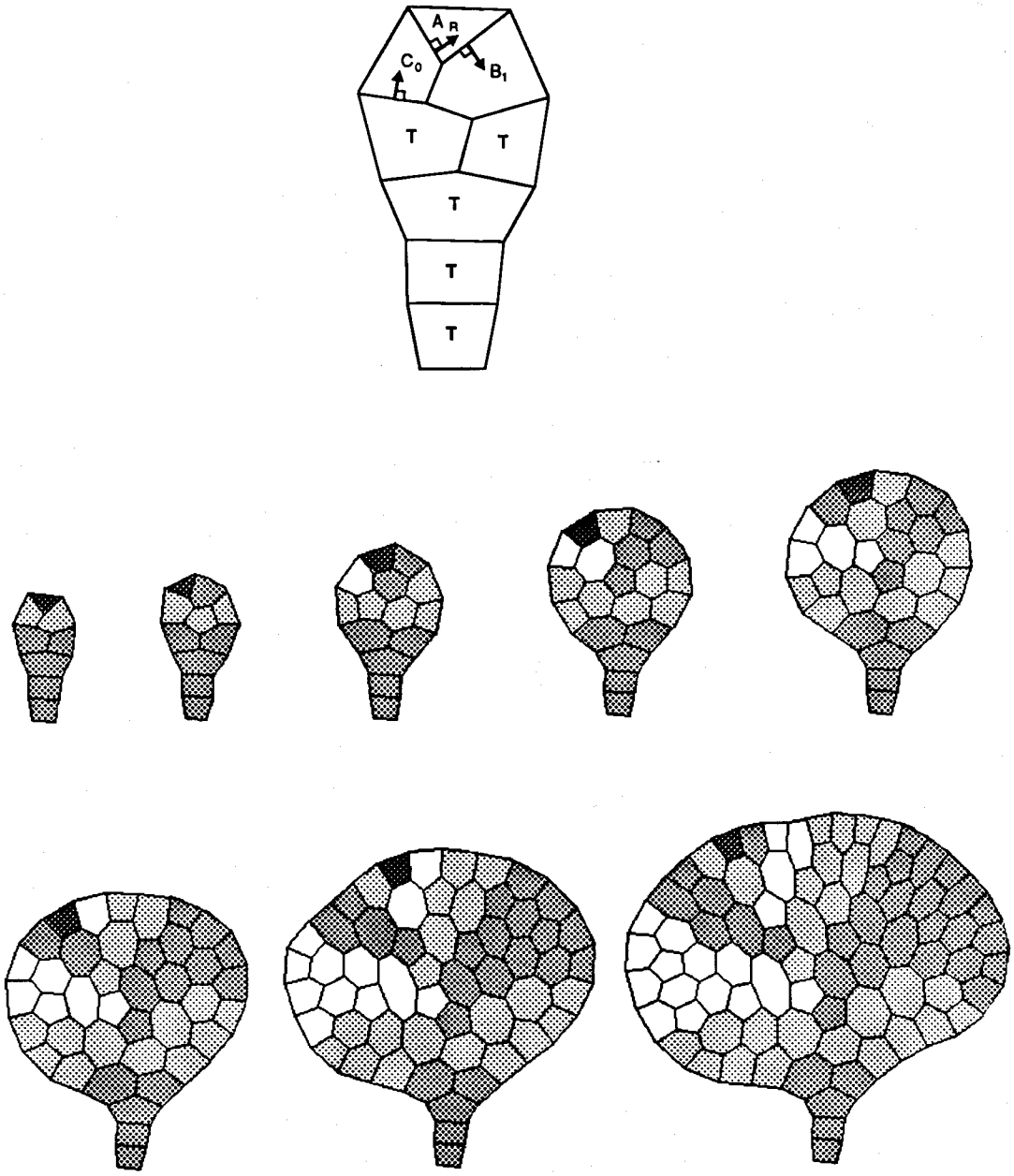

Figure 15: Simulated development of *Microsorium linguaeforme*. (a) The initial structure. Arrows indicate the initial reference vectors. (b) The developmental sequence.

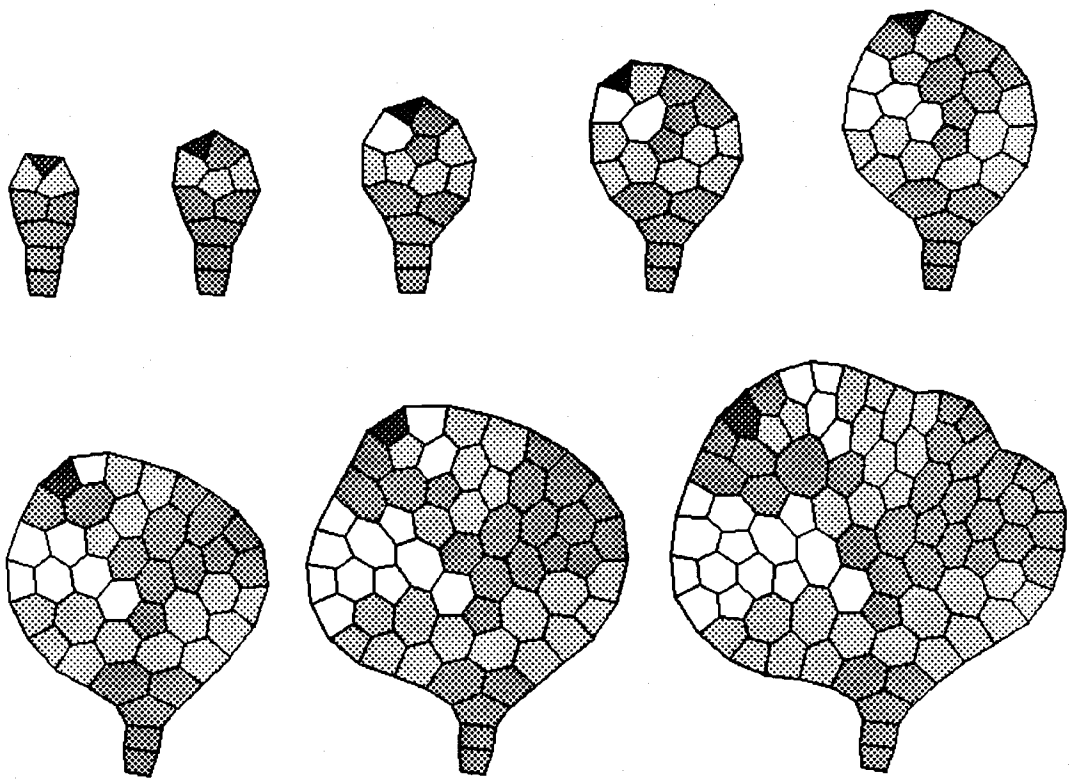

Figure 16: A variant of *Microsorium linguaeforme* thallus

Cell systems operate under the assumption that positions of division walls are controlled from inside the cells. In contrast, map L-systems employ a control mechanism that resides in cell walls. Which mechanism is more justified from a biological point of view is an open problem. Cytological observations of developing tissues reveal that microtubule structures called *phragmosomes*, which radiate from the cell nucleus, coincide with the position and orientation of the division walls [1, 6]. This supports the assumption that the position of the division wall is controlled from inside the cell. Moreover, the polarity vector field corresponds to the notion of *cytoplasmic inheritance* [9], in which the orientation of the phragmosome of a mother cell determines that of the daughter cells. On the other hand, observations do not exclude the possibility that cell walls specify autonomously the attachment sites for the new division walls [9, 13].

The influence of cell shape on microtubule organization, and hence on the position of the division wall, is also supported by observations [6]. This influence may account for topological irregularities exhibited by many cell patterns found in nature. In addition to the variability due to different positions of cells in a structure (Figure 15), cell systems can also capture topological variations resulting from different timings of cell divisions (Figure 17).

Many problems related to cell systems are open for further research. For example, globally defined parameters incorporated in the pressure-tension model impose identical physical properties on all cells. Cell systems with the properties specified locally for individual cells could lead to more faithful models of some structures.

Furthermore, the exchange of information between cells may play as important a role in the development of cellular structures as the lineage mechanism considered in this

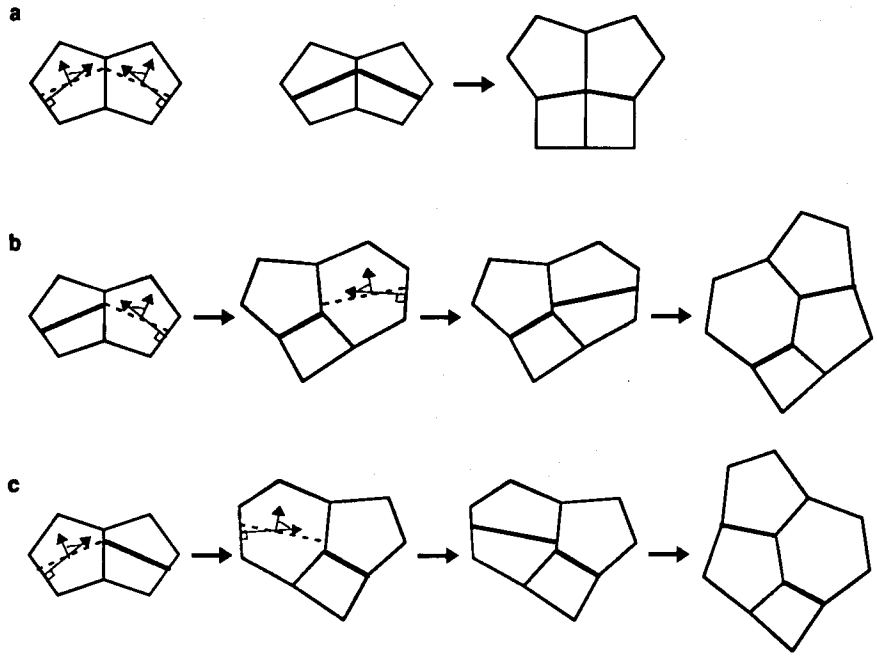

Figure 17: The relationship between the order of cell divisions and the topology of the resulting structure. (a) Left and right cells divide simultaneously. (b) Left cell divides first. (c) Right cell divides first.

paper. A convenient framework for the investigation of patterns that result from the interactions between cells in developing cell layers may be offered by cell systems with context-sensitive productions.

Acknowledgements

We are indebted to Prof. Aristid Lindenmayer for having inspired our research into mechanisms governing cellular development. The reported research has been supported in part by an operating grant and equipment grants from the Natural Sciences and Engineering Research Council of Canada, and by a research grant from Apple Computer, Inc. Facilities of the Department of Computer Science, University of Regina, were also essential. All support is gratefully acknowledged.

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