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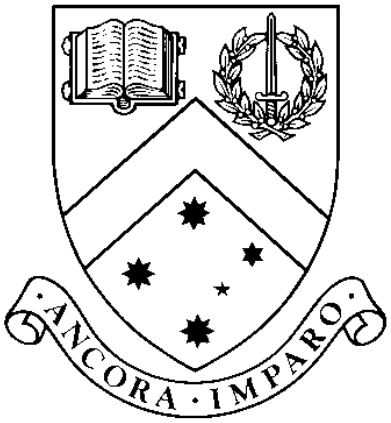

Confirmation Report

A Developmental System for Modelling Organic Form

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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.
D'Arcy Thompson [82, p79]

Contents

1 Introduction

The discipline of computer graphics has boomed over the last two decades, driven by the film, video game, and design industries. The need for more complex, realistic and detailed models has driven research into texture synthesis, rendering techniques, and geometric modelling. It has become increasingly evident that the complex geometries of organic form require new and different techniques. Generative methods, and specifically developmental systems, have been successfully applied in creative domains, however much research still needs to be done. These systems have not been completely adopted into mainstream modelling because of their non-intuitiveness, complexity, or restriction to specific domains. The goal of this research is to develop and successfully use a new developmental system built specifically for the synthesis of complex organic forms, such as those illustrated in Figure 1.

This confirmation report proposes research, and presents some current work, into a new system for modelling organic form. Properties of organic form are outlined first (§2) followed by a discussion of existing developmental systems and their limitations (§3). Some ideas and research questions regarding a new system are then outlined and a timeline for the research proposed (§4).

2 Modelling Organic Form

The complexity of biological organisms far surpasses anything man-made. The geometric intricacy and variety unique to life has inspired scientists, mathematicians, and artists to study, model and reproduce these forms. Computer-aided modelling of organic form is applied in disciplines such as architecture, industrial design, computer games, films, and art. The design of useful methodologies to construct complex forms such as those illustrated in Figure 1 is an important goal and is pursued by this research.

2.1 Modelling Methodologies

Surface modelling is the most common method in geometrical modelling and involves the manipulation of vertices on a polygonal surface, the manipulation of control points of an interpolated surface (see Figure 2), or the use other higher level tools (such as the virtual sculpting of ZBrush [57]). These systems give an extremely fine-level of control and are conceptually elegant, but have numerous problems when modelling organic or complex forms. Firstly, complexity is an issue in these systems, as generally the amount of work required is proportional to the number of vertices or detail of the surface. Secondly, models are usually constructed in isolation which makes this method unsuitable for modelling sets of interacting forms. Thirdly, the created *model* is the *geometry*, which means that semantics in the model is lost and must be manually added or bound to the geometry. An example of this is the concept of *vertex groups* which allows the identification of groups of vertices of a polygonal mesh in order to isolate semantic parts (e.g., leg, head, eye).

The explicit construction of geometry quickly becomes tedious when dealing with highly complex models, and seems vastly inappropriate when the model being constructed has a concise description. High-level descriptions of structures can be used to synthesize geometry [83, 71, 23]. This approach is easy to use and supports complex shapes and properties such as symmetry, variation, and modularity (Figure 3 illustrates a complex tree shape and the corresponding model). As the model is synthesized from

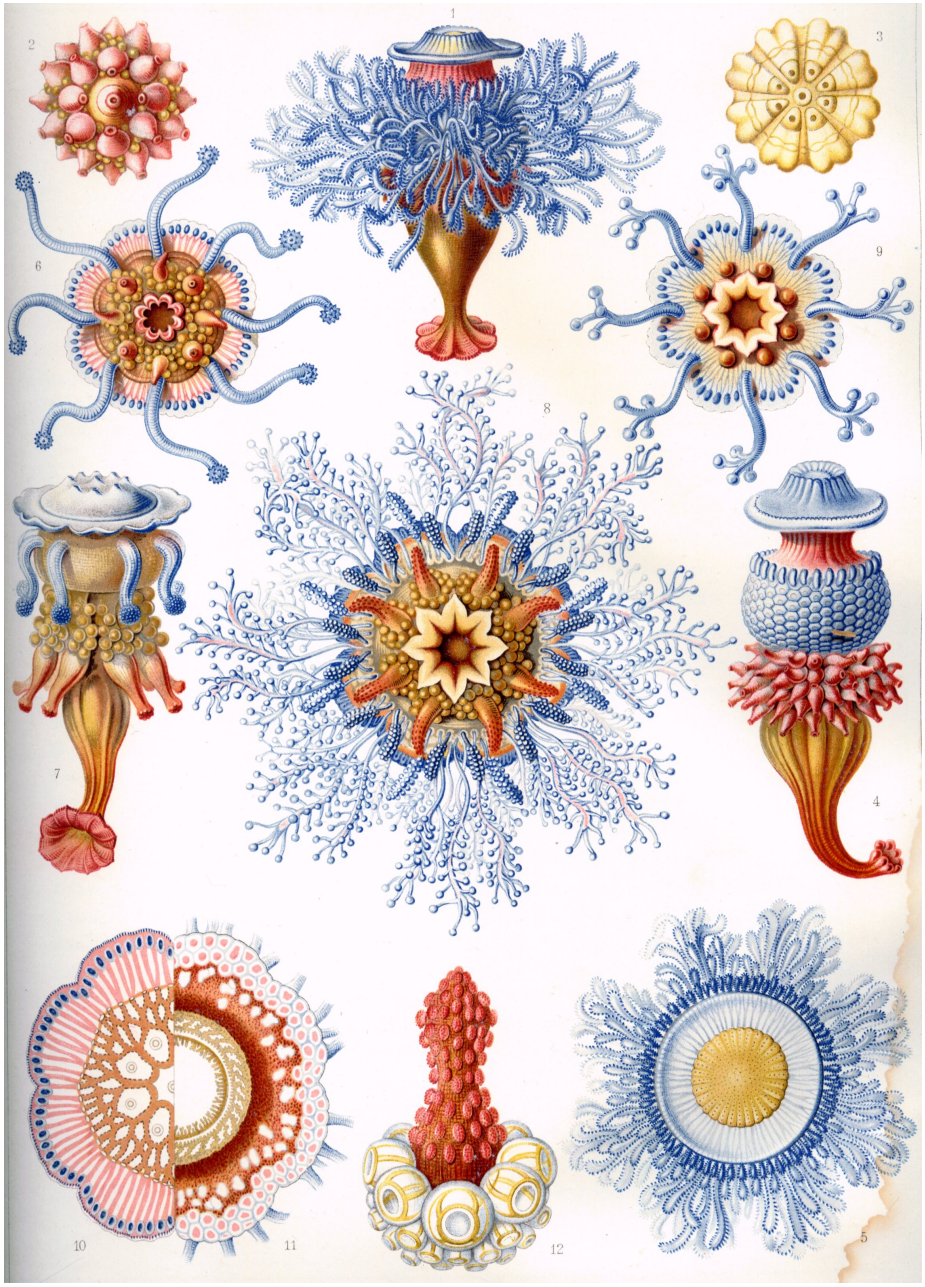


Figure 1: Haeckel's illustrations of Siphonophorae ([24, Plate 17])

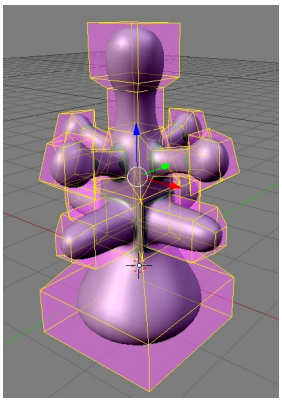


Figure 2: A subdivision surface. A coarse mesh controls the surface of an organic looking object.

the description the complete semantics of the model remains, which provides many benefits, including context-dependant synthesis, easy integration of intra-species[1] variation, and varying level of detail.

These systems are difficult to tune as there are usually a large number of parameters for a complex model (though using the aesthetic mutation/evolution metaphor [83] can alleviate this somewhat). The problems with these methods in their current implementations is that the user is constrained to the set of primitives in the system (there is no method of building new primitives) and there is limited interaction *between* components. For example, Figure 4 illustrates that the spatial interaction between a trunk and its branch is extremely naïve and not at all reflective of the underlying growth process binding the two. The method of creating a high-level description and synthesizing geometry from it is quite powerful, however the implementations so far have been quite simple using descriptive terms that are generally nothing more than specific geometric primitives or transformations.

Generative systems are an alternative approach to form synthesis. The general concept is to design a procedure that *generates* a complex structure. This is analogous to the execution of a computer program, the simulation of some natural process, or the development of an organism. The generative systems that closely resemble the process of biological development are called *developmental systems*.

Developmental systems (in particular, Lindenmayer or L-Systems) have been successfully applied to the generation of complex plant-like forms (Figure 5). In many respects they are a dichotomous approach to high-level modelling as they abstract and simulate the low-level interactions of biological development. These systems abstract the process of growth over time, and have many benefits, such as *database amplification* (the ability to generate complexity from a small description), complex interactivity between components, concise descriptions, time-varying sets of developing structures, and environmental awareness. The primary disadvantage is that a large conceptual gap exists between the model and the form it generates, making the creative process less intuitive. The limitations of these systems are discussed in more detail later (§3).

Developmental systems are a powerful method of generating complex form and provide many benefits over other current methods. This research attempts to resolve

[1]The term *species* is used here to refer to the set of objects with identical descriptions or models.

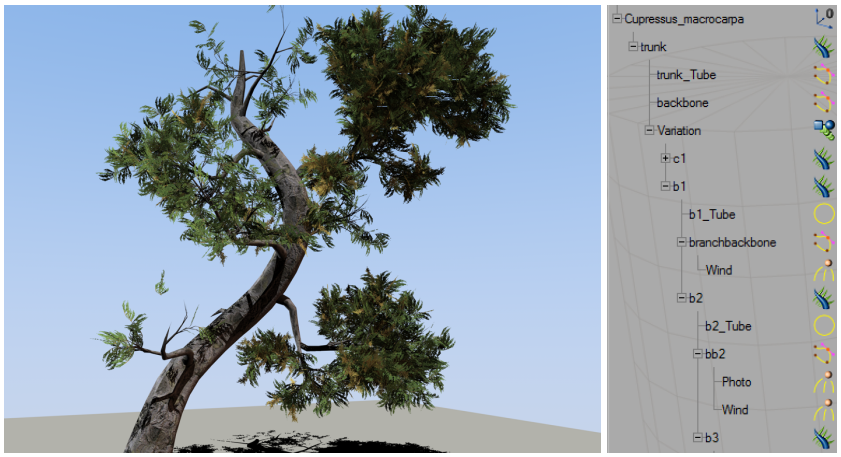


Figure 3: *Left:* A complex model built with XFrog (*Cuspressus* example from http://www.xfrogdownloads.com/Walli/ retrieved 25/03/2008.) *Right:* The high-level description. The model consists of a *trunk* object with a specific profile and branches generated by the *variation* object. The variation object randomly selects one of its children, allowing structurally different branches to be distributed on the trunk. Some other objects of note are the tropisms (wind and photo).

Figure 4: A close up of Figure 3 illustrating the crude interface between trunk and branching.

some of the issues of developmental systems by designing a usable developmental system that can be used to generate shapes of a kind described in Section 2.2. Developmental systems are reviewed in Section 3.

Figure 5: A complex structure evolved using L-Systems. (McCormack, J. *Morphogenesis Series #11*, Lightjet print on archival paper, 1.5m x 1.5m, 2006.)

2.2 Organic Form

The beauty of nature is exemplified by the illustrations of the naturalist, biologist and artist Ernst Haeckel (1834–1919). *Kunstformen der Natur* [24] provides many excellent archetypes (e.g., Figure 1) for the type of form this research is attempting to model. Haeckel's illustrations are schematic rather than realistic [63], and it is this quality that makes them suitable for defining properties of organic form. This section elaborates on the concept of organic form as defined for this research.

If we consider the abstract shape in Figure 6 we can attempt to elucidate the properties of it which make it seem *organic*. At a brief inspection it has a smooth appearance, a distinct head-tail axis, is radially symmetric (around a curvy axis), has a donut topology, and has bulges. It has a distinct main *body*, and tentacles which are similar and arranged in a tight packing around a particular band of the body. The tentacles themselves are bulgy smooth cones that have a distinct, dynamic and curvy axis and are seamlessly growing out of the body. The tentacles in the back are a lot more complex and have sub-tentacles growing out of them. From this description we can identify many properties such as symmetry, modularity, materiality, hierarchy, physicality, and growth. A formal definition assists the direction of the research.

A mathematical definition: A *shape* in three dimensions is a compact set whose boundary is a smooth surface. In other words, a shape is a solid smooth three dimensional form. Note that this definition excludes objects such as fractals, points, lines,

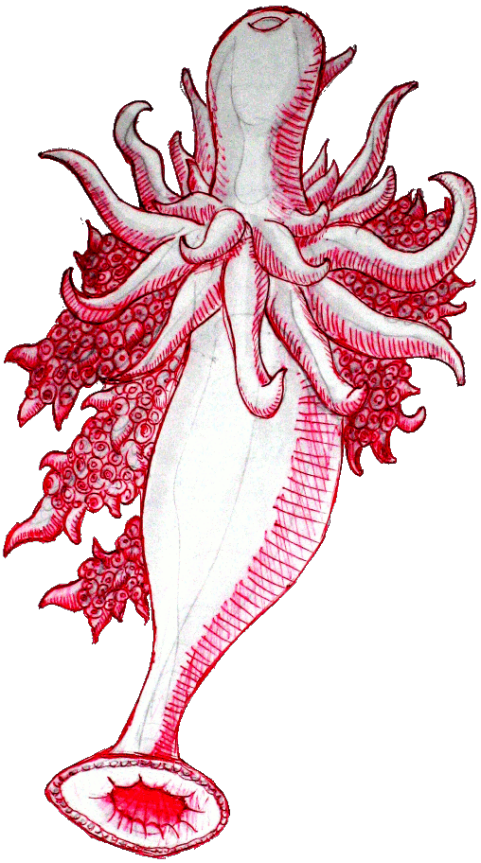


Figure 6: The author's replication of one of Haeckel's illustrations [24, Plate 7: *Siphonophorae*].

infinitely thin shells, rough surfaces, and discontinuous surfaces. We classify an *organic shape* as a shape that has one or more of the following properties.

Symmetry Symmetry is the property of sameness. Most organisms are either bilaterally, radially, or phyllotactically symmetric [34]. Some organisms are segmented and have translational symmetry. Self–similarity exists in organisms, as well as other natural forms [47]. Symmetry in natural systems is not as precise as the mathematical definition of symmetry, and usually variation over the symmetric transformation and between symmetric parts occurs. A modelling system should provide a mechanism for producing the above mentioned approximate symmetries with a fair amount of control over variation and symmetry type.

Hierarchy *Molecules, Amino Acids, Proteins, Organelles, Cells, Tissues, Organs* and *Organisms*: this is a natural hierarchy constituent in all animals. Evolution results in hierarchical organisms due to the inherent stability of hierarchical systems and con-

struction [70]. At a visual level we can divide an organism up into a body, limbs, hands, fingers, *etc.* This spatial hierarchy is also a temporal one when considering the process by which these structures are developed. Flexible spatial and temporal hierarchies require a model that is limitless in the expression of detail on many scales.

Modularity Modularity is common to organisms in the form of limbs, cells, and organs, for example. Modules are important as a design tool as they help encapsulate and interface sub–shapes or logic in design. The organic, physical and epistemic boundaries of modules in organisms are sometimes well-defined (e.g., a skull) but usually not (e.g., the boundaries of a limb seem undefined). Developmental systems usually have defined concepts of modularity, however it is usually the emergent and ill-defined modules that a user is interested in. Recognising and isolating these parts would be a useful mechanism, but is a very difficult problem and has not yet been considered in any implemented system. An artist using a system should be able to create and identify modules, should be able to model a shape with specific modules in mind, and have some control over the geometric or semantic interfaces between modules.

Physicality *Physicality* refers to the features of shape that imbue it with a sense of physical existence. We can identify two separate contributors to this: the materiality of the shape and the environment it inhabits.

Referring back to our discussion of Figure 6 we referenced terms such as bulgy, smooth, and axis. These are material properties of the organism. Other terms describing materiality include: worn, eroded, fractured, rough, hairy, amorphous, and brittle, however this research is concerned only with the properties of *soft* and volumetric shapes like our archetype in Figure 6. Modelling systems have only recently appeared [57, 3, 9] that incorporate materiality. Materiality in developmental systems has been investigated with appealing results [35].

The notion that an environment exists is lacking in most modern form modelling tools. In systems such as Xfrog [23] the environment is grossly abstracted into simple idealised equations. Few systems incorporate interaction in space [36, 22, 85, 67], this is primarily due to the computational complexity involved. Competition and interaction in space helps arrange and give a strong sense of existence to form.

Topological Complexity Organisms are complex dynamic arrangements of cells and matter, so ascribing a notion of topology to them is pointless. However, if we abstract the skin (ecto- and endoderm) of an organism into a continuous surface with a solid volume between, we can start to topologically describe them (Figure 7). We are also concerned with the arrangements of modules and the relationships between them. Our archetype (Figure 6) illustrates a complex set of spatial relationships that are dynamic over ontological time. An appropriate modelling system would have to be flexible in its modelling of spatial and temporal relationships.

L–Systems (§3.3) are powerful generative systems but are limited to branching topologies. It is the goal of this research to design a system that is able to describe more general topologies.

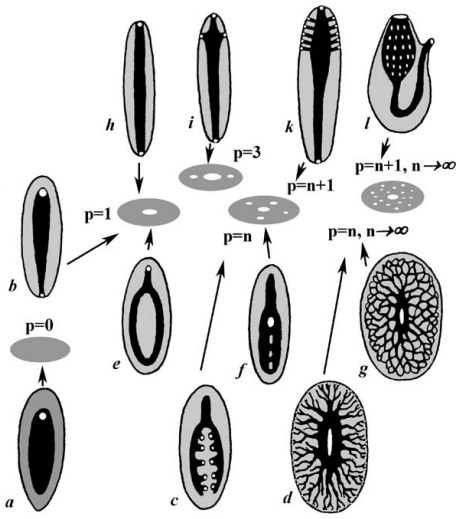


Figure 7: Some topologies of different species of flat worms, hemichordates and lower chordates. From [33, p2060].

3 Developmental Systems

Biological development is arguably the greatest success of nature. The self-construction of an extremely complex multi-cellular organism from a single cell is a powerful phenomenon. The study of the initial stages of development, *embryology*, can be traced back to Aristotle in the fourth century B.C. [21, p5]. More recently, interest from abstract [45], creative [61] and applied [73] point of views has led to the study of *developmental systems*: abstract systems that attempt to achieve the same representational efficiency, generative capability and robustness of organismal development.

There are numerous established systems from theoretical biology, computer graphics and artificial embryology that model structure or form and incorporate aspects of biological development. Important surveys that cover these models include [43, 66, 20, 59, 58, 73, 41, 17, 6]. This section reviews the most relevant systems with a consideration of the applicability or extensibility of these systems to model organic form.

3.1 Cellular Automata

The cellular automata (CA) approach is a simulation-based modelling methodology that uses discrete time and space (and often state). Ermentrout and Edelstein-Keshet [17] survey some biological applications and identify three main types of CA: deterministic (von Neumann and Ulam's original formalisation), *lattice gas* models, and *solidification* models.

Deterministic CAs represent the system as a regularly connected set of (usually finite state) automatons, which change state depending on the state of neighbouring automatons. The concept of cell and space are one and the same, and it is generally the case that an empty space is represented as a cell in a particular state. One of the first and simplest models of cellular growth via accretion is the *Eden model* [15]. Branching growth in CAs was studied by Ulam [86]. These ideas have been applied to computer graphics to synthesize three dimensional form [22, 39]. Lattice gas and solidification

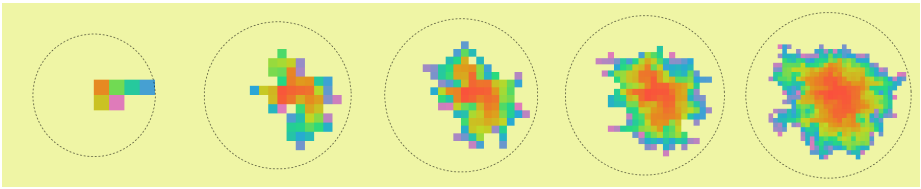


Figure 8: An example simulation of the Eden process at 5, 50, 100, 200, and 500 time steps. Simulated using [90].

Figure 9: Some realistic examples of Greene's voxel space automata. [22, Figures 5 and 9]

models discretise space and model cells and molecules that move between sites. These models have been used extensively to model various phenomenon, including growth by diffusion limited aggregation [89], cell sorting [29, 30] and limb formation [8].

Eden The *Eden model* was introduced by Eden [15] to model the population growth of cell colonies. The process begins with a single cell on a regular lattice and iteratively grows the *colony* by adding a new cell at a site adjacent to the colony (determined stochastically). The colony grows dense clusters with fractal surfaces (Figure 8). This model is one of the simplest growth models possible.

Greene Greene's *voxel space automata* models the growth of a structure through a discretised three dimensional space. At each time step, the growing structure attempts to add a new *part* to itself according to some set of rules (like available light, proximity to some object, the result of an intersection test, *etc.*) Greene observed that some complex structures arise (see Figure 9) through the interplay of probabilistic growth, environmental effects, and feedback between the growth rules and space.

This model illustrates the expressive power inherent in a spatially embedded developmental system: the growth rules are simple, yet complex relationships arise from the coupling between the rules and the space they act on. However, this model lacks the ability to express detail across spatial scales (as it is tightly bound to its discretisation of space) and is limited to accretive (boundary) growth. This makes it inadequate for generating organic shape (as defined for this project §2.2.)

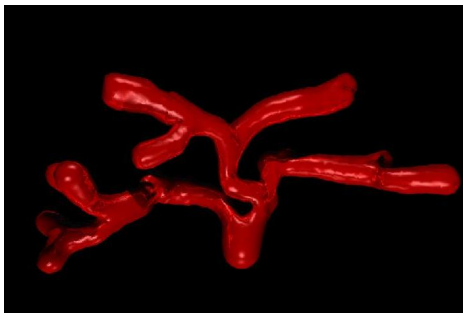


Figure 10: One example of Kaandorp's generated forms (original from http://staff.science.uva.nl/ jaapk/example95.jpg retrieved on 27.03.08).

3.2 Kaandorp's Coral Model

A developmental model of accretive growth that illustrates the combination of a geometric surface-based developmental model with a physical model of nutrients and hydrodynamics is presented by Kaandorp and Kübler [36, 37]. The work is biologically motivated but successfully illustrates a model of surface growth and physical simulation.

The developmental process is initialised with a triangulated sphere. A *growth process* then repeatedly constructs a *new* triangulated surface around the old one. This method is particularly interesting as it does not attempt to modify the old surface but merely adds a new layer on top. This is conceptually appropriate for the accretive growth processes it models. One growth process [37, §4.6.4] assumes that food particles are dispersed throughout the environment via diffusion and hydrodynamics and that local growth is proportional to the concentration of food particles. A physical simulation is performed to compute the distribution of food.

These experiments, when taken out of their biological context, reinforce the notion that a simple growth logic combined with a physical model can result in complex and organic forms (Figure 10). Kaandorp's work is oriented towards the validation of biological models of growth but could easily be applied to creative modelling.

3.3 L-Systems and Grammars

3.3.1 L-systems

L-systems were introduced by Aristid Lindenmayer [45] in order to describe the development of multicellular organisms. Lindenmayer proposed that these systems could integrate and express many facets of development including: gene control mechanisms, cell lineages, organising centers, polarity, and allometry [28, Preface].

L-systems model cells as symbols and development with *rewriting rules*. An organism is represented as a string of symbols that develops through a process of parallel rewriting. Different symbols denote different cell types or states. Developmental processes such as division, differentiation, cell death, cell movement, and cell communication are all modelled by rewriting rules. The simplest class of L-systems are the *deterministic*, *context-free* L-systems, denoted as D0L-systems[2]. A simple example

[2]The 0 (zero) stands for zero-sided. The alternatives are D1L and D2L-systems which, respectively, allow one-sided and two-sided context dependant rules.

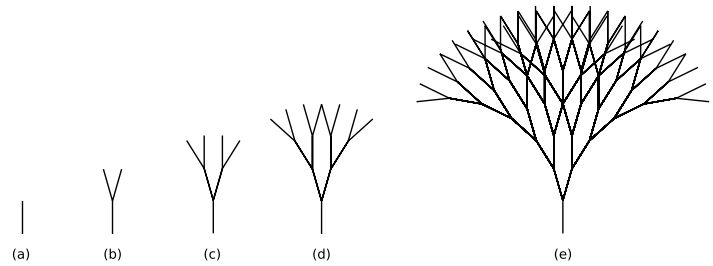


Figure 11: A D0L-system $\{\omega : F, F \rightarrow F[+F][-F]\}$. The interpretation of the symbols are: F move in current direction one step while drawing, $-/+$ turn left/right 16 degrees, '[' push the current position onto the stack, ']' pop the last position off the stack and move there. The sequence of drawings corresponds to the sequence of strings generated by the system after (a) 0 steps, (b) 1 step, (c) 2 steps, (d) 3 steps, and (e) 6 steps.

which has the alphabet $\{a, b\}$, the axiom a, and a single transition rule is:

$$\omega : a \tag{1}$$

$$a \rightarrow ab \tag{2}$$

We assume an extra rule exists that leaves b unmodified, i.e., $b \rightarrow b$. The sequence this system generates is $a, ab, abb, abbb, abbbbb, \ldots, ab^n$, where b^n indicates n concatenated b's. L-systems were quickly adopted into formal language theory[3].

L-systems can be used to synthesize shape by considering the symbols as drawing instructions. The turtle-based interpretation is the most common method and uses the concept of a drawing *turtle* or machine. The turtle exists in the drawing space and reads each symbol in sequence performing commands such as *draw line*, *turn*, *change colour*, *store current position* or *reset position*. Figure 11 illustrates an example. As a form generating tool, L-systems are extremely powerful [61], furthermore they have paralleled other grammar-based approaches to modelling shape. These include *shape grammars* [75], *collage grammars* [13], *graph grammars* and grammars that operate on polygonal surface representations.

L-systems are conceptually elegant as they use a simple but expressive abstraction of development. From the perspective of computer science these systems are fast (as they operate on symbolic strings) and are extremely expressive (context-sensitive L-systems are Turing complete). However to generate realistic images various extensions need to be used. These include the integration of continuous mechanisms [60, 59], the modelling of physical and mechanical effects [35, 42], specifying explicit hierarchy [87, 51] and coupling the developmental process more closely to the environment [56]. These extensions solve various issues but they corrupt the simplicity and elegance of the original formalism.

Some of these extensions attempt to tighten the coupling between the discrete symbolic *representation* space of L-systems and the continuous space and time they are *interpreted* in. The difference between these spaces results in various issues, two of

[3]By considering the set of all organisms generated by a particular set of transition rules as a language we can explore the generative power of various L-systems. One particularly interesting result is that context-free Chomsky grammars form a proper subset of context-free L-systems. See [28, 64, 65] for a comprehensive survey of results in this field.

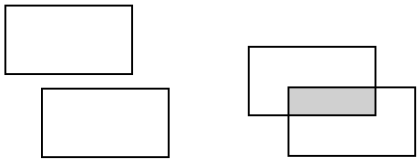


Figure 12: Translating the upper rectangle on the left image down by some amount creates an emergent rectangle (highlighted in grey).

which limit these systems being applied to the generation of organic form. Firstly, the topologies of the generated forms are tied to the topology of the representation[4]. Secondly, the interaction amongst components in the interpretation space is not reflected in the representation space (e.g., the overlapping lines of Figure 11(e) are not reflected in the symbolic description), requiring extra scaffolding to bind them more closely.

3.3.2 Other Grammars

The term *grammar* has been applied so broadly that it now loosely refers to any system whose changes can be described using sets of replacement rules that replace one component, sub-structure, sub-shape or schema with another.

Shape Grammars Shape grammars [76] are a formalism for describing transformations on shapes. A shape grammar usually consists of an axiomatic shape and a set of transformations that act on shapes[5]. It differs fundamentally from other grammar-based systems as it works directly on shapes, rather than symbolic representations of shapes. This makes systems difficult to implement because they require shape recognition and an extremely flexible internal representation. Shape grammars are inherently more powerful than symbolic systems due to ambiguity within shapes and the emergence of new shapes (Figure 12). This feature makes shape grammars ideal for art, architecture and product design where emergent shapes contribute greatly to the aesthetic.

Shape grammars have been applied to the design of Palladian houses [77], Chinese Lattices [74], Coffee Makers [1], and Coke Bottles [7], amongst others [7]. It is useful to analyse the process of constructing these grammars, as they provide a practical application of reverse engineering a set of shapes into a (relatively) concise grammar specification. Shape grammars demonstrate the powerful consequence of having representation and interpretation exist in the same space. This concept is referred to as *embeddedness* in this report, and is a key component of the proposed system.

Polygonal Surface Grammars L-systems and grammar-based approaches have been extended to operate on polygonal surfaces [27, 46, 72]. These address the topological limitation of L-systems and provide generative methods for complex surfaces. These methods have been applied to the generation of architectural and biological shapes,

[4]For example, strings are one dimensional, which constraints their practical representational ability to one dimensional or tree structures.

[5]The term *shape* here is rather loosely interpreted but is usually restricted to a formally constructed object from primitives (points, lines, polygons, surfaces, *etc.*)

however none have incorporated the ideas of embeddedness, physicality, or the biological development analogy. Surface-based representations are more expressive than string-based representations but still lack the ability to model internal growth and the resulting physical effects.

3.4 Matela's Triangulated Graph Model

Triangulated graphs have been successfully used to model cellular layers and applied to theoretical studies of cell self-sorting [48, 49, 50, 62]. This research was specifically targeted at modeling cellular layers, of which a two dimensional approximation was adequate. Other representations have been investigated including using Voronoi [31] and polygonal regions [88].

General Model Matela and Fletterick's general model [48] uses a planar map to model sheets of cells: regions represent cells and edges represent cell boundaries. The resulting complex then approximates cells of polygonal shape that are densely packed (see Figure 13.) Allowing cells to have an arbitrary polygonal shape is the primary rationale behind the development of this model, as it provides greater flexibility over previous (hexagonal or rectangular grid-based) models in topology, cell size and cell shape [48].

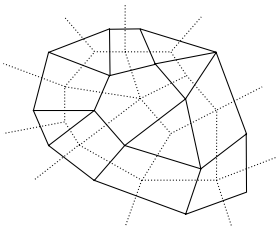


Figure 13: A cellular layer. Cells are modeled as densely packed polygons. The topology of the complex is given by the dual of the map (the dotted graph).

When reasoning about the model it is conceptually simpler and more mathematically tenable to consider the dual of the cell map rather than the map itself. Under this interpretation we consider cell layers as planar graphs where cells are nodes and edges indicate neighbourhood relationships. In this formal model there are three basic operations that do not modify the cells: insertion, deletion and exchange of edges (see Figure 14).

Triangulated Model Matela and Fletterick show that the general model results in unstable networks from a biological perspective [48]. They restrict their attention to a specific instance of the model: the triangulated graph (or trivalent map). This reduces the set of primitive operations to the single operation of *edge exchange* (since the other operations would void the triangulation requirement.)

Using just this operation and two cell *types* it was shown that cell self-sorting can occur under different conditions [49]. The model was later extended to incorporate cell division [50] and death [14]. The rules for cell division where based on a series of *division masks* which combinatorially enumerated all possible subgraphs in which a cell might divide and provided a transformed subgraph for each. The rules attempt

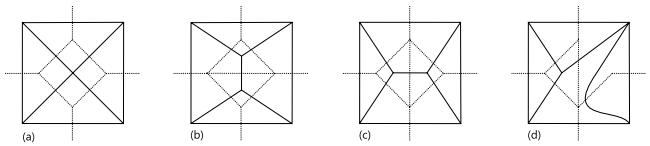


Figure 14: A cellular layer (a) has an edge inserted (b) resulting in a change in topology. It then undergoes an edge exchange (c) and an edge deletion (d). These cases demonstrate the effects of the primitive operations of the topology (dotted graph) and the conceptual cell map.

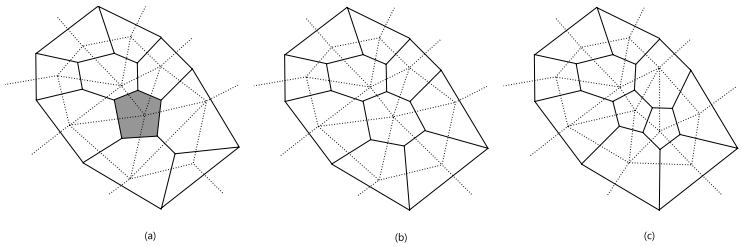


Figure 15: A cell complex (a) with a migrating cell (shaded). The cell moved towards another cell in (b) (modelled as an edge exchange) then divided in (c).

to balance out the neighbourhood links of a dividing cell equally between its daughter cells.

Matela *et al.* noticed that this division mechanism often resulted in cells with very large numbers of neighbours, so they provided a balancing mechanism that allowed cells with more than nine neighbours to locally rearrange themselves through edge exchanges[50]. Figure 15 depicts a complex cell layer with an edge exchange followed by a cell division.

Extension To Three Dimensions Ransom and Matela [62] present an extension of this model to three dimensions, however it is still limited to cellular layers and generally not applicable to more complex shapes. The extension and embedding of this model within three dimensions is the structural and geometric basis behind the proposed developmental model.

3.5 Artificial Embryology

The study of abstract developmental systems is known as Artificial Embryology (AE) (and is also known as Computational Development or Artificial Ontogeny). It is driven by the need to autonomously create very complex systems such as neural networks, robots, and other systems by harnessing principles in biological development. AE is primarily concerned with the *evolution* of these structures rather than building them via a user-directed creative process. We consider a select few systems from AE to illustrate different developmental abstractions (a recent survey categorises others [73]).

Streichert *et al*. presents a complex system that grows groups of cells [78]. They evolve the organisms to be limited in their growth (i.e., to grow to a certain size and stop) and to self–repair if damaged. Their model incorporates continuous space, is structure–oriented, and has dynamic neighbourhood relations between cells. Cell be-

haviour is controlled by Random Boolean Networks (RBNs) and S-systems. They also implement endogenous communication between cells. Their model incorporates a simple physics in which cells have a uniform size and attempt to attach to their seven closest neighbours. Adhesion forces the cells into stable configurations. This structural model is simple and elegant, however an extension to three dimensions does not seem plausible.

Fleischer developed a continuous, mechanism–rich framework that integrates mechanical interaction (collision, adhesion) and intracellular processes (transcription, regulation, kinetics, transport, metabolism, a cell surface protein model, cell lineage, cleavage plane control, neurite growth, and electrical activity) [19]. This model incorporates the connectionist ideas of Mjolness *et al.* [55] and illustrates a method of abstraction that is closer to physical reality than other systems. Fleischer used his system in an evolutionary way, attempting to evolve simple structures with concepts of modularity, hierarchy, and symmetry. This system is more suited to generating networks of interacting components (like a neural network) than geometric form.

Dellaert and Beer explored the evolution of a developmental model for autonomous agents with a simple morphology and control system [12]. Their model is divided into the organism, cell, and biochemical levels. At the lowest level the *DNA* is represented as a bit vector where the *genes* are the individual bits and have an *on* or *off* state. The dynamics between the genes are modeled by an RBN. Each cell contains a bit vector indicating which genes are active, this is updated at each time step using the current state and the state of its neighbours (iterated repeatedly until the network enters a stable state.) The cell divides if a certain gene is activated. Other mechanisms, like communication and differentiation are also included. A key result of this paper is that the evolution of the agents effectively reinforced and extended a developmental pathway (in the RBN) that eventually built successful agents. This research presents an extremely abstract model of cell division, differentiation, communication, and gene regulation that motivates the interesting question of what is the appropriate level of abstraction in a developmental system.

Eggenberger describes an AE system that can generate interesting and simple shapes out of connected cells [16, 32]. His goal is to evolve simple forms through the interplay of a simple developmental system, evolution, and a simple physical environment. He notes that the inclusion of an artificial physics assists the evolutionary process in finding specific forms. This balance of development and physics is emphasized in this research project.

3.6 Morphogen Models

Turing showed in 1952 that complex patterns can arise from simple systems of interacting chemicals or *morphogens* [84]. Turing postulated that these *reaction-diffusion* systems exist in biological systems and assist in coordinating the spatial expression of genes. This has recently been confirmed [69]. These systems have been investigated deeply [53, 54] and applied to the creative synthesis of complex patterns (Figure 16) [85, 67]. More recently, these systems have been coupled to geometry to investigate morphogen-directed growth [25, 44, 10].

Leung and Berzins present an interesting computational model of development [44]. They link concepts of cell bio-chemistry and surface deformation to model simple developing shapes (Figure 17). Their model uses a reaction-diffusion simulation of morphogens on a surface. The surface curvature is locally altered by the presence of morphogens, thus tightly coupling the surface geometry and cell chemistry. This

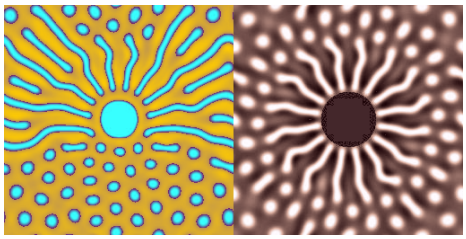


Figure 16: A complex reaction-diffusion pattern (original from [67, Figure 15].)

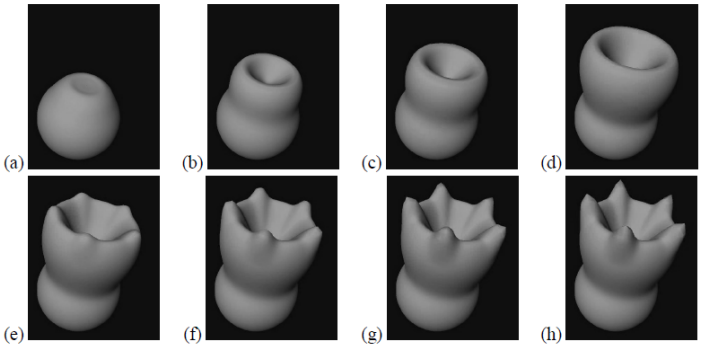


Figure 17: Leung and Berzin's model of a developing polyp (from [44, Figure 9]).

system successfully demonstrates that patterning combined with surface alteration can produce organic forms.

These systems are targeted at demonstrating principles in theoretical biology, and are not creative systems. Their application to the creative modelling of organic form is hindered by a few reasons:

- the reaction-diffusion process is notoriously hard to control;
- these systems lack important developmental processes such as apoptosis, mitosis, and migration;
- the geometric representations prevent topological changes; and
- growth is limited to the surface;

3.7 Conclusion

The reviewed systems demonstrate that the developmental metaphor is a powerful technique when modelling form or process. The goal of this research is to apply this metaphor to the creation of complex and organic form and demonstrate a working system. The systems reviewed are all, at some level or another, too limited for the specific research goal. With these limitations in mind we present five main principles that guide the development of a new system:

embeddedness the representation and interpretation of shape spatially co-exist;

geometrically expressive the representation can approximate arbitrary organic shapes (as defined in §2.2);

biological relevance the system should have facilities to efficiently and accurately implement models from biology;

physicality aggregate or differential effects of physical forces should be easily incorporated; and

efficiency the system should be fast, and can trade-off *accuracy* for *usability*.

We now present some ideas for a new developmental system.

4 A New Developmental System for Modelling Organic Form

This research project involves the design, implementation and analysis of a developmental system that supports the generation of complex organic geometry. Research and experimentation to date has led to a preliminary design and partial implementation of a new system, the *simplicial developmental system* (SDS). Further research is still required to expand the detail and compare design choices in this system. This system uses processes from biological development and physics to *grow* three dimensional solid forms that have the properties outlined in Section 2.2. It is inspired by a number of models from theoretical biology [48, 53, 53], computational development [78, 19, 2], and computer graphics [61], and attempts to address the major limitations inherent in previous systems (§3). The model incorporates physical effects such as adhesion, elasticity and spatial constraints that help organise the shape and drive development. The theoretical basis of the model has foundations in engineering, computational geometry and theoretical biology.

This section describes the components of SDS, including the shape representation, transformation rules, physical constraints, and the mechanisms underlying cell communication, organisation, and autonomy. Two models from biology already implemented in this system are presented. Finally some interesting further research questions are posed.

4.1 Structure

The structural aspects of SDS build upon the triangulated graph representation of cell layers (§3.4) and extensions [62, 14]). The proposed system generalises it to the concept of a pure simplicial n-complex in n-space controlled by adhesive cells competing for space. Compared to the original model, the domain of use and advocacy for the representation is different, since we are not bound exclusively by biological relevance[6]. The rationale for this representation is driven by computational, geometric, and physical constraints.

[6]The gap between the real and artificial should ideally be small for the sake of implementing models.

4.1.1 Representation of shape

Numerous theoretical and computational models of shape exist, including interpolating representations, implicit and explicit surfaces, iterated function systems, and constructive solid geometry (see e.g., [5],[18, §7],[68, §9.7],[4] and [52]). We outline some discrete methods and motivate the choice of the simplicial complex as the representation sheme of SDS.

Discrete models The representation of shape by collections of discrete elements is a common strategy in computer graphics.

Polygonal surface representations approximate surfaces with basic connected elements such as triangles or polygons. It is applied primarily in the geometric modelling, computer graphics, and film industries. Modern graphics hardware deals with this representation natively and numerous creative applications exist that directly support this model. *Subdivision surfaces* (see e.g., [91]) extend this model with mechanisms to help approximate smooth surfaces and handle varying levels of detail. Some grammar-based generative systems have been developed that work with this representation (§3.3.2).

Volume discretisation methods use simple solid components such as cubes, hexahedra or tetrahedra. The voxel approach (§3.1) is an extremely fast and conceptually simple method; however, its major disadvantage is that it cannot represent multi-scale detail well. Tetrahedralisation of volumes is more flexible and has been successfully used in the popular *Finite Element Method* of computer-aided engineering. Recent techniques for realtime physical simulation of tetrahedralised volumes [80] have popularised this representation.

The discrete representation is the most appropriate for a form generating developmental system. Most of the systems reviewed (§3) use a discrete representation as the correlation between cell (or homogenous module) and discrete element provides an elegance and simplicity to the conceptualisation and implementation of developmental models. Moreover, the local specification of discrete elements and resulting aggregate form maintain a close biological relevance (§3.4). The concept of a *simplicial complex* generalises the tetrahedralisation and triangulation representations, and is used as the geometric representation of shape in SDS.

4.1.2 Simplicial Complexes

An *m-simplex* is defined as the convex hull of a set of $m+1$ affinely independent points (i.e., no three points are co-linear, no four points are co-planar, *etc.*) Hence, a triangle is a 2-simplex and a tetrahedron a 3-simplex. A simplicial complex is a set of simplices with the restriction that the intersection of any two simplices is a point (0-face), edge (1-face), or face (2-face). Furthermore, a *pure simplicial k-complex* is composed only of k-simplices and their intersections, it is this restricted type that forms the shape representation scheme of the system (see Figure 18).

Restricting our attention to two and three dimensional space, these structures are sets of edge-connected triangles (in 2-space) and face-connected tetrahedra (in 3-space). Approximating surfaces or volumes with simplicial complexes has numerous benefits over other representations. These include:

- conceptual simplicity;
- generality (can be used in an arbitrary number of dimensions);

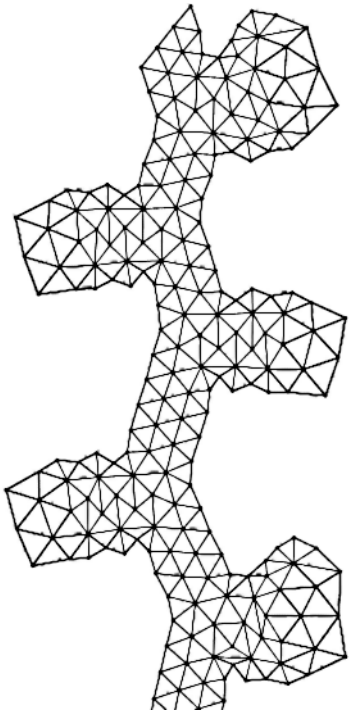


Figure 18: A pure simplicial 2-complex.

- computational efficiency;
- support of multi-scale detail;
- flexibility (can approximate arbitrary volumes and model complex topologies); and
- the support of modern tools (many current tools support operations on this representation, hence the developmental system could readily be integrated into such tools).

SDS in n dimensions uses the n-simplex as an abstraction of a homogenous part of a developing system. A pure simplicial n-complex represents a multi-cellular system. Conceptually, the shape is a solid entity that has spherical cells at the vertices of the simplices with the edges defining a direct-contact relationship between cells (see Figure 19). The size and shape of the simplices are governed by the sizes of the cells, as discussed later §4.3.

4.2 Transformational

Early development consists of processes such as: cleavage divisions, pattern formation, morphogenesis, cellular differentiation and growth (see e.g., [21]). We are primarily concerned with *morphogenesis*, the process by which cells proliferate, organise and form complex structures. The fundamental processes that drive morphogenesis are (from [21, p13]):

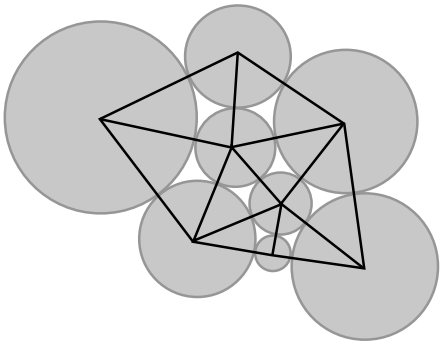


Figure 19: A set of cells and the corresponding simplicial complex.

- cell division;
- cell shape changes;
- cell movement;
- cell growth;
- cell death; and
- changes in the composition of cells and secreted products.

These fundamental operations on the simplicial representation are now defined. The core operations in SDS that modify shape include cell division, cell growth, cell movement, and cell death. These rules are given explicitly for two dimensions and are based on Matela's model §3.4. The three dimensional rules are yet to be formally defined and constitute part of the ongoing research.

4.2.1 Cell Division

Cell division, or *mitosis*, involves a complex process of genome duplication and membrane cleavage [21, p111]. It is this simple action that provides the multitude of cells that constitute a multicellular organism (a *Metazoan*). Most developmental systems use an axiomatic notion of cell and thus incorporate a *division* operation.

In the proposed system, there is no concept of nucleus or membrane, and the content of the cytoplasm is abstracted to a set of continuous values (see §4.4). Division is abstracted to a process that replaces one cell with two daughter cells each half the size of the parent and with a distribution of state variables governed by the cell program. This division is usually symmetric.

We assume that upon cell division the two daughter cells are adjacent. We also require a direction or axis of division[7]. The complex topology of the representation requires that the local connectivity of the mother cell be distributed and reorganised around the daughter cells, and here we follow Matela's approach §3.4 by requiring that the distribution is as equal as possible. A distinction is made between internal division and division on a boundary.

[7] In a cell program this direction could be omitted, where it would then be computed to be the direction of least resistance (i.e., the direction that results in the system with least energy).

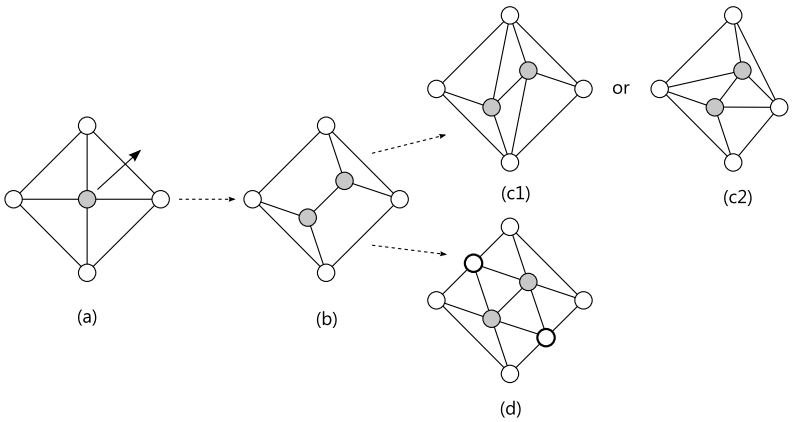


Figure 20: The process of internal cell division with an even number of neighbours. (a) The cell has elected to divide in the direction shown. Using the direction of division we (b) divide the mother's neighbours into *front* and *back* and connect them to the daughter cells. We reach a situation where the local structure must be re-triangulated. We can do this in two ways. By (c1 or c2) assigning an equal number of neighbours to each daughter. This results in one of two situations which can be selected based on some criterion (e.g., minimise total length of edge connections). (d) The alternative is to create a more symmetric topology by adding extra cells.

The general division procedures provide two alternate methods: one that uses *stabilising* cells, and one that doesn't. It is currently unclear which method is more appropriate, hence both are presented. The final system will incorporate one of the two alternatives.

Internal division Figure 20 illustrates the division of a cell internal to a complex. Two alternate methods are proposed. One key part of this research is to investigate both methods and determine which is more suitable for the application domain. If a cell has an odd number of neighbours and divides then an asymmetric distribution will occur. We abstract the notion of "direction of division" to "division *into* an attached simplex", as illustrated in the formal procedure for division given in Figure 21.

Boundary division There are two types of boundary division, *along* the boundary, and *away* from the boundary (Figures 22 and 23).

Stabilisers The division rules mentioned above give two alternate rules: one that includes special balancing cells, and one that excludes them. It is not yet obvious which method is more appropriate for two dimensional and three dimensional systems. The inclusion of these *stabilisers* results in increased structural complexity and stability (it seems) in the growing shape; however, they also raise a few semantic issues. The biggest problem is: *what should the active genome and state of these stabilisers be?* We *could* attribute to them an interpolated state of their neighbours, however this may result in cell programs that are hard to control or specify. The alternative option is to reserve a special *stabiliser gene* that is activated upon their introduction.

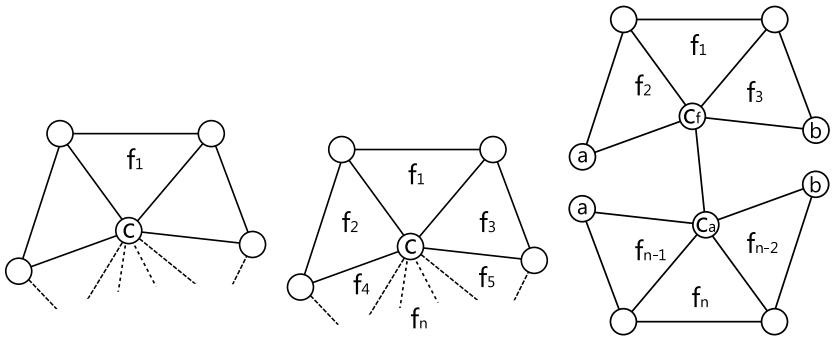


Figure 21: A cell division algorithm. (a) The input to the procedure is an internal cell c and an adjacent face f_1. The cell can have an arbitrary number n of neighbours. (b) The first step is to order the remaining $n-1$ faces $f_2, \ldots, f_n$ using a breadth–first traversal of the adjacent face neighbourhood graph. (c) Remove the mother cell and replace it with two connected daughters denoted the *fore*, c_f, and *aft*, c_a, cells. The faces are divided equally among the daughters with faces f_1 to $f_{\lfloor n/2 \rfloor}$ connected to c_f and faces $f_{\lfloor n/2 \rfloor + 1}$ to f_n connected to c_a as shown. If n is odd then c_a will have one more connected face than c_f. We identify the cells a and b, which form part of new simplices (a, c_f, c_a) and (c_f, b, c_a).

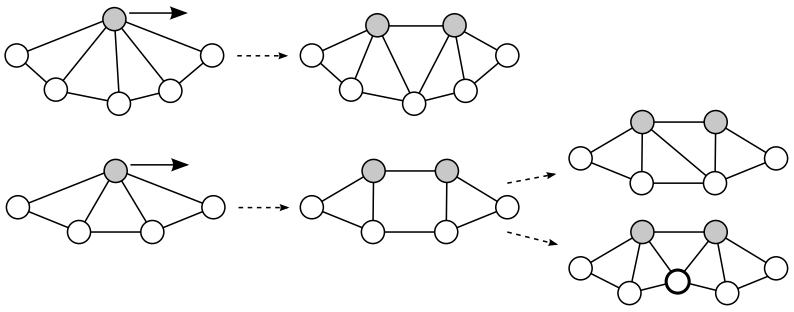


Figure 22: Cell division on a boundary. Division along the boundary. The upper figure demonstrates the trivial division of a cell with an odd number of neighbours. The lower figure illustrates a non–triangular region that can form when dividing, which can be re-triangulated either asymmetrically or with a peripheral stabilising cell.

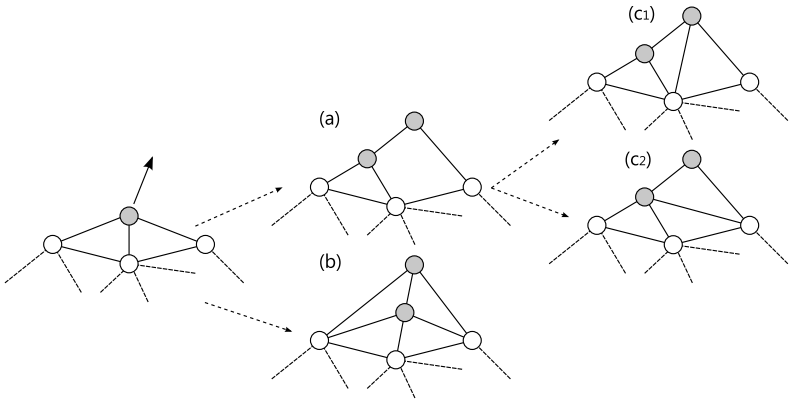


Figure 23: Cell division on a boundary. Division away from a boundary results in two cases, (a) one-sided or (b) symmetric. A one-sided division results in a quadrilateral which must then be triangulated into either (c1) or (c2). Note that (c1) is the more stable configuration as the all cells have more than two neighbours.

An appropriate default behaviour for the stabilisers is to be unresponsive to stimuli, diffusing any protein that enters it (behaving essentially as empty space). The cell could self-destruct if it deemed the surrounding space *stable*, or could merge together with other stabilisers it came into contact with, leading to a larger, simpler structure.

4.2.2 Cell Growth

Cell growth combined with mitosis results in a massive change in size during development. Different rates of growth (*allometry*) are evident in developing organisms (for example, a comparison of a human baby to an adult reveals a proportionally different skull size). Some developmental systems ignore this [12] but for an abstraction of morphogenesis cell growth is essential.

The capability of the simplicial complex to represent detail on many scales is only useful if mechanisms are in place that can modify the size and shape of the simplices. Cell division is one mechanism, cell growth is another. SDS abstracts cells as perfect spheres with a centered point mass. The system can control the radius and mass of the cells. This is done through two state variables $\frac{dr}{dt}$ and $\frac{dm}{dt}$ which can be input to or output from the cell program (see §4.4).

4.2.3 Cell Movement

The movement of cells in an organism or developing embryo is an important process in its self-assembly. Cell movement supports: the aggregation of dispersed cells; the relocation of groups of cells; the dispersal of locally manufactured cells around the organisms; and the formation of connective cell networks [11, p96]. It has been extensively demonstrated that cell movement (through differential adhesion) can self-organise specific structures and patterns [48, 30].

The model of movement of cells used here is essentially the same as Matela and Fletterick's model (§3.4). They consider cell movement as the addition or removal of edges, which in a triangulated system can be reduced to the *exchange* of edges. In

addition to this, Duvdevani-Bar and Segel [14] consider the positions of cells and allow cells to move through space while undergoing neighbour exchange.

Two dimensional movement is illustrated in Figure 24. A cell can elect to move through space, and in doing so the topology of the complex changes around it. The fundamental operation of the edge-exchange is applied here as described in Section 3.4.

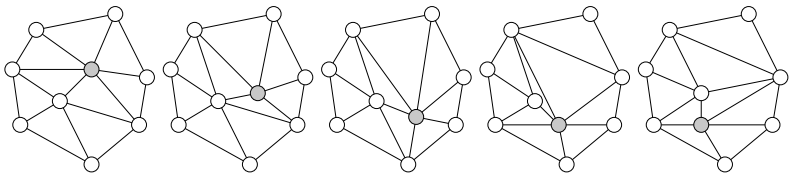


Figure 24: Cell movement through space and the exchange of edges.

Conceptually, cell movement in three dimensions uses the same ideas as the two dimensional case, however the edge-exchange operation is more complex. Edges can belong to more than two simplices and, as Figure 25 demonstrates, local manipulations can propagate throughout the mesh.

The explicit exchange of neighbouring cells has not been considered with respect to the triangulated graph representation. Trivially it involves swapping two adjacent cells. This form of cell movement is more abstract and possibly more appropriate for our circumstances. However, a problem with this method is that it involves a discrete jump in the state of the system that may destabilise the simulation.

4.2.4 Cell Death

The death of a cell can arise necrotically from poisoning, membrane rupture, physical stress and starvation. Cell death can also be a programmed part of development where it is referred to as *apoptosis* [21, pp158–160]. This can be advantageous to an organism by redistributing resources or creating specific structures. The formation of mammalian fingers or toes via death of inter-digital tissue is a prime example of the use of apoptosis [21, pp522–523].

Cell death in the system is based on Duvdevani-Bar and Segel's model [14]. They describe the process of cell death as the slowing down of activity and *successive removal* of connections to neighbouring cells. This procedure uses the edge exchange actions used in cell movement and is described in Figure 26. Apoptosis of boundary cells is trivial.

In three dimensions a cell with four neighbours can remove itself trivially (Figure 27). With more neighbours the procedure follows that of the two dimensional case, sequentially severing neighbourhood connections (via the edge-exchange operation) until it forces itself into a four neighbour state.

4.2.5 Further operations

Additional operations that affect topology could easily be integrated into the system. The system is quite amenable to additional operations, including many which are not biologically motivated, yet may be useful. These include fusing cells together, subdividing regions, and modifying connectivity of cells. The geometric operations could

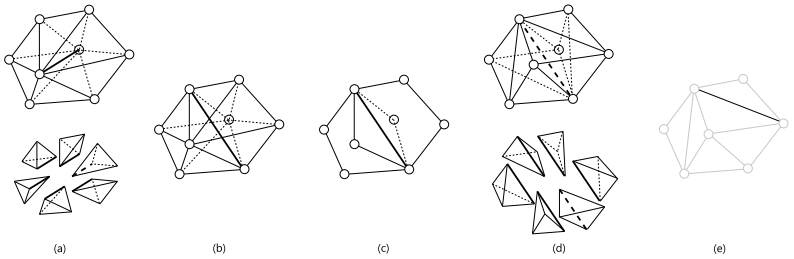
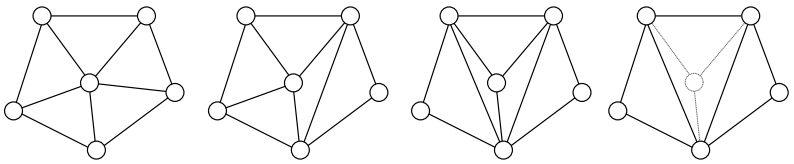
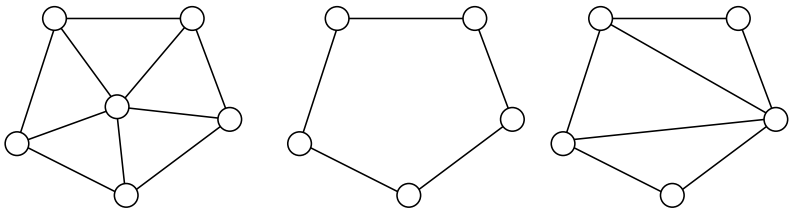


Figure 25: (a) Any edge in a tetrahedral complex can be part of many tetrahedra (six in this example.) An edge exchange operation can be performed by removing the edge of interest and connecting two unconnected vertices (b) belonging to the adjacent tetrahedra. However this invalidates all of the connected tetrahedra (c) so the vertices must all be re-triangulated (d). This may result in other edges being flipped (e) which will then propagate throughout the complex.



(a) Cell death in Duvdevani-Bar and Segels model [14]. The inner cell elects to die and sequentially severs its adhesion to neighbouring cells. Once it has three neighbours it is then destroyed, implicitly preserving the triangulation. In our model this sequence *could* execute over time.



(b) Another approach could be to remove the cell and all connecting edges, then to re-triangulate the local structure. This could incorporate some stability criterion to ensure the resulting structure is appropriate.

Figure 26: Death of internal cells.

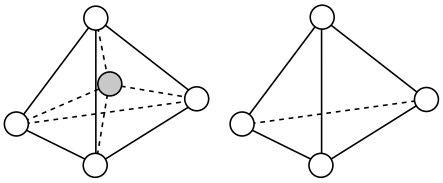


Figure 27: A cell with four neighbours is internal to a larger tetrahedra and so can remove itself without a propagating effect.

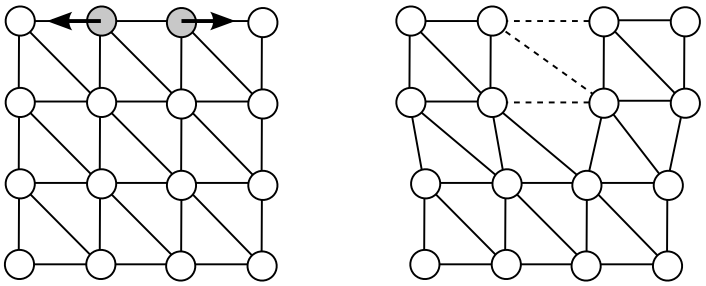


Figure 28: A fracture operator could detect when large forces are separating two cells and remove the edges when appropriate.

be used to refine and clean the mesh or allow an adaptive level of detail. This is out of the scope of the current research however, and is left for future consideration.

Fracture Cell death in the development of autopods (e.g., hands) allows the disintegration of webbing and separation of digits. The cell death mechanism mentioned above (§4.2.4) maintains the local connectivity of cells, and hence by itself would not support a digital separation model. Consider the cell complex in Figure 28 and the possible large forces that are separating the highlighted cells. An operation to remove the links between cells would be beneficial when implementing features such as this.

Adaptive Structure As noted by Matela *et al.* [48] after many divisions the triangulated graph becomes biologically unstable. Their system balances the mesh by forcing cells with large amounts of neighbours to disconnect from the extra neighbours through edge-flipping. The same problem occurs with this representation and it is beneficial to require that the mesh remain as uniformly triangulated as possible. This ensures that it is physically more stable and approximates as best as possible the shape and aggregate effects of cells. The method of Matela *et al.* is appropriate, however it is a purely topological method. Research into maintaining a stable structure constitutes part of this project.

4.3 Physicality and Embeddedness

The physical elements of our world that affect ontogenetic and phylogenetic development include gravity, pressure, surface tension, temperature, radiation, magnetic fields, friction, viscocity, and adhesion. Evolution exploits these physical rules to generate functional forms with minimal cell behaviour. For example, using just differential cell

adhesion Hogeweg demonstrated that a variety of natural patterns such like segmentation and budding could form [30].

Embeddedness was referred to in the previous section with respect to space. To reiterate: the system is spatially embedded because the representation and interpretation of the structure are in the same space. The space in which the shape exists can be extended to include the concept of physics (or other rules about the world). Incorporating physical rules into the output space affects its capability of containing specific forms. We call this *physical embeddedness.* The intrinsic incorporation of these rules is a key feature of this system and is considered vital to shaping organic forms.

The importance of physicality within the space becomes evident when we consider the coupling between the properties of cells, simplices, edges, and the effects of various transformations. This coupling should reflect the properties of the space. To provide a biologically and physically appropriate system a method for linking these variables is established. This method provides:

- *structure and volume conservation*: a growing part of the shape should force its surroundings to expand/organise around it, regions of the shape should resist being compressed, and
- *an overlapping constraint*: no simplices should overlap.

4.3.1 Structure and Volume Conservation

As cells proliferate, move, and die, the effects on the organism are topological, geometric, and physical. A homogenous collection of proliferating cells can be considered as an expanding region that forces other neighbouring regions to change, which in turn propagates further changes throughout the developing embryo. These effects are governed by physical laws.

The effect of cellular actions have been defined topologically, what remains is to define the geometric effects of these actions. The relationship between the geometry of the cells and the simplicial complex first needs to be defined. Loosely framed, the position, size and topology of the cellular complex define the shape and topology of the simplicial complex. The edges of the complex represent the adjacency of two cells, and hence should have a length equal to the sum of the two cell's radii. An ideal situation is presented in the left part of Figure 29 in which the cells can be arranged so the lengths of the edges of the simplices are the same as the sums of the adjacent radii of cells. The right hand side illustrates the more common scenario where this doesn't occur, however the edges still represent an adjacency relationship and so the cells are conceptually being stretched or squashed.

A cell that changes size or position will effect the local shape around it. We model this by giving each edge a preferred size, which is the sum of the adjacent cells' radii. We incorporate *physics* into SDS using the concept of *elastic potential energy*. The energy of the system is:

$$E_1 = \sum_{e \in \text{edges}} kd_e \left|\text{length}(e) - \text{preferredlength}(e)\right|^2,$$

with kd_e representing the strength of the adhesion. Furthermore we can include a volumetric constraint on the simplices that assist in enforcing *nice* simplices. This can be modelled by calculating a preferred volume for each simplex from its adjacent cells,

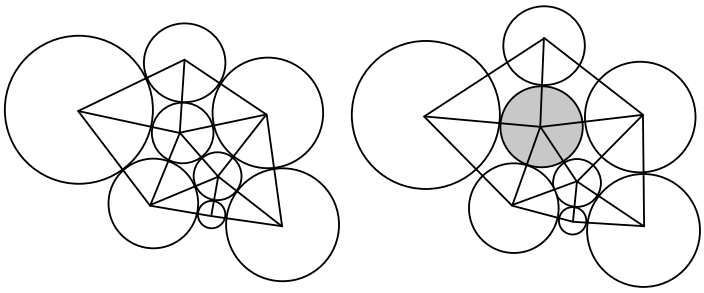


Figure 29: A collection of cells and the simplicial complex representing its topology and spatial organisation. A cell changes its size causing the simplices to be changed.

and then defining a similar energy:

$$E_2 = \sum_{s \in \text{simplices}} kv_s \left| \text{volume}(s) - \text{preferredvolume}(s) \right|^2,$$

with kv_s representing volumetric conservation strength. We then define the *best* shape as the shape which minimises $E_1 + E_2$. Approximating cells as point-masses and using newtonian physics, we can specify the dynamics of the system as:

$$\frac{\partial^2 c}{\partial t^2} = \frac{f(c)}{m_c},$$

for each cell c, where m_c is the mass and

$$f(c) = \sum_{e|c \in e} -\frac{\partial}{\partial x} E(e),$$

summing over all edges and simplicial elements.

Teschner *et al.* provide a method of local volume and structure conservation [80] that uses a similar model, is conceptually elegant, fast, and supported by fast collision detection and analysis [79, 26]. The algorithms underlying these methods have been implemented and constitute the physical component of the three dimensional implementation of SDS.

4.3.2 Spatial Constraints

An important physical property of the system is that no two elements overlap in space. The mathematical description of shape requires that no two simplices overlap in space. The volume and structure constraints specified above *do not* maintain this constraint. The fast collision detection and penetration depth algorithm by Teschner *et al.* [79, 26] has been implemented in the system. This ensures that no cell penetrates an element. This technique is not exact but provides a visually acceptable and fast approach to approximately enforcing the overlap constraint.

4.4 Information, Communication, Organisation and Autonomy

The success of development relies heavily on the ability of cells to organise and coordinate their actions. This requires cells to be able to disseminate, obtain and process information.

4.4.1 Communication

Cells communicate via the use of proteins and receptors which bind to them. Once bound the receptor releases another protein internal to the cell which results in a series of reactions usually ending in the activation or repression of a particular gene. Signalling can also occur by passing proteins through special *gap junctions* in the cell membrane of adjacent cells. As an abstract mechanism we can considered proteins as messages that move through an organism and modify the behaviour of cells. Interaction of proteins can generate patterns [69] (postulated by Turing in 1952 [84]), this *reaction-diffusion* mechanism has been heavily explored in mathematical models [53].

The coordination and organisation of the developing embryo and complex organs such as the vertebrate eye [21, p143] rely extensively on communication amongst cells. The diffusion and decay of protein throughout cellular or syncytial complexes can set up morphogenetic gradients which cells can use to infer coordinate systems or positional information [21, pp63–66]. Many aspects of shape in organisms rely on these gradients hence SDS incorporates a continuous signalling mechanism that abstracts protein diffusion.

In our developmental system we assume the following

- There is a finite set of proteins;
- Every cell accepts and diffuses *all* proteins;
- Cell membranes are negligible;
- Protein can be manufactured or destroyed (from nothing) in a cell;
- Proteins transport around the organism via diffusion (at a protein specific diffusion rate); and
- Proteins decay over time.

To model the diffusion of proteins through the shape we need to balance simplicity and accuracy. Figure 30 illustrates some different alternatives. Option (b) provides the simplest approach capable of modelling morphogenetic gradients. This results in the following assumptions about the biological relevance of this model:

- Proteins only exist *inside* cells where they can be measured by a continuous proportion (0 empty, 1 full);
- Signalling is juxtacrine[8], occuring only between adjacent cells along edges of simplices; and
- Diffusion is isotropic.

Diffusion of protein occurs between cells and degradation of protein occurs within cells. These are modelled together using the Fickian law of particle diffusion:

$$\frac{\partial P}{\partial t} = D_P \nabla^2 P - C_P P,$$

where D_P is the diffusion rate of the protein and C_P is the decay rate. This is discretised according to the selected diffusion approximation (in this case: Figure 30(b)) and assumptions.

[8]Cell signalling in early development can be categorised as juxtacrine or paracrine. Juxtacrine signalling occurs between two neighbouring cells by passing proteins through gap junctions in the shared membrane, and paracrine signalling involves diffusing proteins through the extracellular matrix (over short distances).

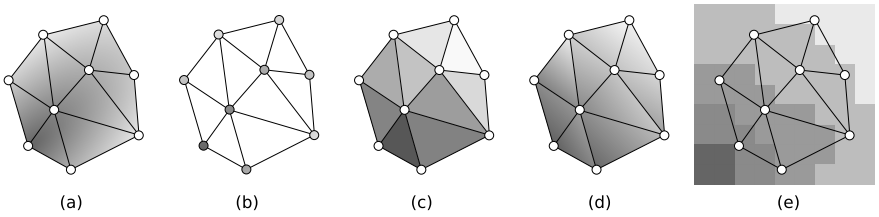


Figure 30: (a) The ideal model, where protein diffuses continuously throughout the shape. The simplest approximation to this is to (b) restrict the protein to be internal (and uniformly so) to cells. Alternately, we can model the protein internal to the simplices and either (c) constant across the simplex or (d) varying. Another approach would be to (e) discretise the space the shape is inhabiting and use that to model the protein distribution.

4.4.2 Autonomy

The universal abstraction in developmental systems is that of the *autonomous cell*. There are many different models of cellular autonomy, all abstracting the role of the genome and the effects of proteins. We can identify some different general schemes, which from most abstract to most biologically appropriate are machine (turing, program, automaton), grammar, regulatory network, and connectionist.

Some systems use an imperative programming approach (e.g., the Cellular Programming Language [2]). The cell is conceptualised as a computer that communicates and executes logical instructions in sequence. An alternate approach could be to use a parallel communication calculus (such as Π-calculus) that would be more appropriate in modelling the complex highly parallel nature of gene regulation and development.

L-systems implement autonomy through rules that execute based on context, cell type and state. Given a cell with a particular type, state, and context, the grammar encodes a replacement rule that acts on that cell. There are a finite set of rules and types, however (parameterised) state may be continuous.

An abstraction that is closer to biology than all these methods is the Genetic Regulatory Network (GRN). Each cell has a finite set of genes which are active or inactive. Active genes can cause the production of protein, activate or repress other genes, and can be activated or repressed by protein thresholds. The coupling between genes and proteins is then described by a network. More abstract forms of these networks (Random Boolean Networks, or RBNs) have been identified to contain interesting dynamics (see e.g., [38]) and used in artificial embryological systems [12].

The *connectionist* approach of Mjolsness, Sharp and Reinitz provides a phenomenological framework for modelling development [55]. Their approach abstracts collections of interacting cells, proteins and genes. It integrates continuous dynamics with grammar-based rules of cellular actions. The general idea is to define a matrix T^{ab} of continuous values that defines the interaction between genes a and b, where a positive value indicates activation, a negative value repression, and a zero value no interaction. Other assumptions about the system (e..g, that gene effects are approximately additive) lead to a set of simplified differential equations describing the dynamics of the system. This system has been used to model and evolve primitive neural networks and shapes out of cells roaming on a plane [19] and extended to more accurately model development (e.g., [40]).

These last two approaches seem better suited to the continuous messaging framework argued for in the previous section. As the developmental system develops it should become clear what the advantages and disadvantages of these approaches are, and whether higher-level constructs (sub–networks, sub–matrices) can help to design particular forms. At the time of writing, research into the feasibility of these mechanisms in SDS is yet to be undertaken.

4.5 Implementation and Examples

SDS has been partially implemented. A two dimensional system has been implemented that incorporates cell division, growth, movement, mesh balancing, simple physics (a basic spring model along edges), protein diffusion and decay, and simple cell programs. Key features to be completed are the overlapping constraint, cell death, and volume conservation physics. Nonetheless, several models of development have already been implemented using the system (§4.5.1,4.5.2) and serve as basic proofs of concept.

A three dimensional system has also been partially implemented. At the time of writing this has a fast scheme of structure and volume conservation, along with collision detection and response. The methods used are closely based on the recent real-time soft-body physics papers of Teschner *et al.* [26, 79, 80, 81]

Some examples demonstrating SDS and the implementation of some biological models in it are now presented.

4.5.1 Drosophila–like segmentation

Segmentation is the process by which some form is divided into parallel bands. It occurs primarily along the principle axes of the shape, however, as is the case with Drosophila the principal axes are usually *defined* by the segmentation process. This is a powerful mechanism as *arbitrarily shaped form* can then be segmented without the explicit specification of any coordinate system or axis.

The early development of *Drosophila melanogaster* is well studied and provides a useful model of segmentation. We will consider an abstract model concerned only with antero-posterior segmentation and the expression of a single band.

Initial Configuration Consider the initial configuration as a homogenous collection of cells. *Drosophila* development essentially begins with the insertion of maternal factors (mRNA and proteins) into the anterior side of the egg. Applying this to our model we have the initial configuration shown in Figure 31 (the protein shown here is representative, and should be considered internal to the adjacent cells only.)

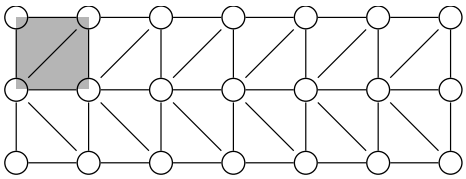


Figure 31: An abstract *Drosophila* embryo with maternal factors (the shaded regions.)

Antero-posterior gradient development The maternal factors include *bicoid* mRNA which is responsible for the antero-posterior axis formation. After translation of the mRNA the Bicoid protein diffuses and degrades eventually forming a morphogen gradient along the antero-posterior axis. This can be modeled on the developmental system using protein diffusion (Figure 32).

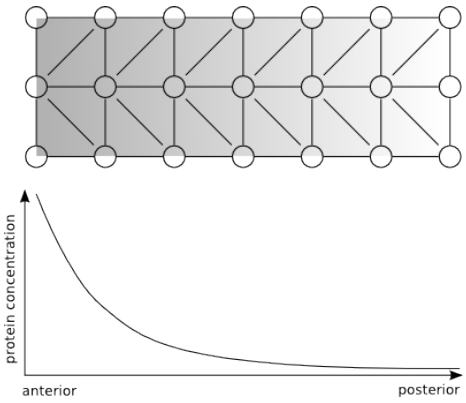


Figure 32: After some period of simulation the Bicoid protein has diffused and set up a concentration gradient.

Segment formation Bicoid activates the *hunchback* gene in the anterior of the egg which produces *Hunchback* protein. The diffusion and degradation of this protein sets up a hunchback antero-posterior concentration gradient. The *Krüppel* gene has two thresholds: a Hunchback concentration that activates it, and a Hunchback concentration that represses it.[9] If the Hunchback concentration is between these two thresholds the gene is activated. This model in SDS uses a simple regulatory network as shown in Figure 33.

Implementation Figure 34 demonstrates an example execution of the implementation. The model accepts an initial shape and insertion of maternal product P_1 into an arbitrary location. P_1 is used to set up a region that autocatalyses the production of another protein P_2 which performs the same function as the Hunchback protein in the model above. The region of *Krüppel* gene activation (refer back to Figure 33) is specified via the *steady state* of Hunchback. To model this we add another internal protein P_3 which is catalysed by P_2 at a rate that regulates the time of activation of the growth action.

This model results in various parameters: diffusion and degradation rate of each protein, activation and repression threshold for each interaction, rate of growth, and rate of protein synthesis. By altering the parameters of the model, the isolated segment can be modified both in size, position, and time to activation. These parameters are not all independent and it would be a useful task to reduce it to a smaller set of (dimensionless) parameters. The research will investigate issues such as these and attempt to design *useful* and *robust* phenomenological models of organic shape.

[9]Modelling a protein concentration P_A that activates *and* represses a gene G_A at different levels can be thought of as abstracting a more complex process. For example, P_A activates G_A at level a, P_A activates G_B at level b, G_B causes the production of P_B which immediately represses G_A, hence from our perspective P_A activates G_A at a and represses it at b.

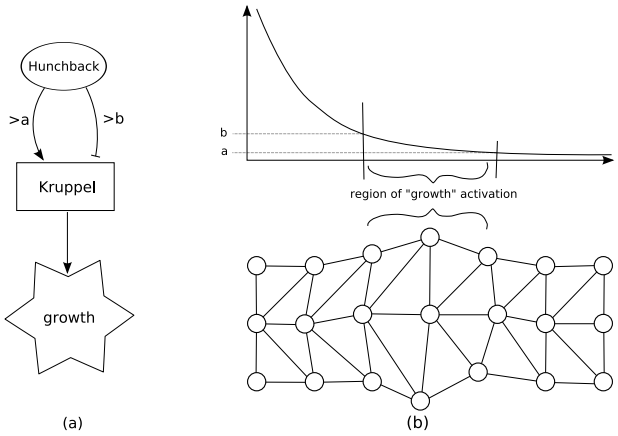


Figure 33: (a) A simple logic showing the relationship between Hunchback protein, Krüppel gene and a cell action. (b) The effect of this program.

4.5.2 Limb development

The proximal-distal growth and differentiation during early limb development is the result of interactions between the epithelium (a primitive skin) and mesenchyme (free floating cells) beneath it. In brief, the apical ectodermal ridge (AER) is a small bump on the epithelium that induces the underlying mesenchymal cells (via the protein Fgf8) to differentiate and produce Fgf10, which induces the AER to create more Fgf8 (Figure 35).

The model of limb growth is interesting as it contains a feedback loop that sustains development and uses local induction to direct growth. A simple model has been implemented (Figure 36). Note the tumour-like growths, these arise as the model is essentially uncontrolled growth biased towards a certain direction.

5 Plan

The nature of this research falls into two streams, work on SDS and the study, implementation and analysis of biological models of development. These streams inform each other, but can proceed independently to some extent. The research will be iterative in the biological stream (research a model, abstract it, implement it, analyse it) and incremental in the developmental system stream (observe bad behaviour, fix model, add a new rule, etc), the former driving the latter. The short-term research goals are quite clear and presented here. A general outline of the tasks needed for the longer project are also given. An estimate of the time required for each component is given, based on experience from the partial implementations and experiments, and the biological and technical literature studied. The tasks are divided into four categories, based on the stream of research they belong to. Some further or contingent research questions and directions are given in the next section.

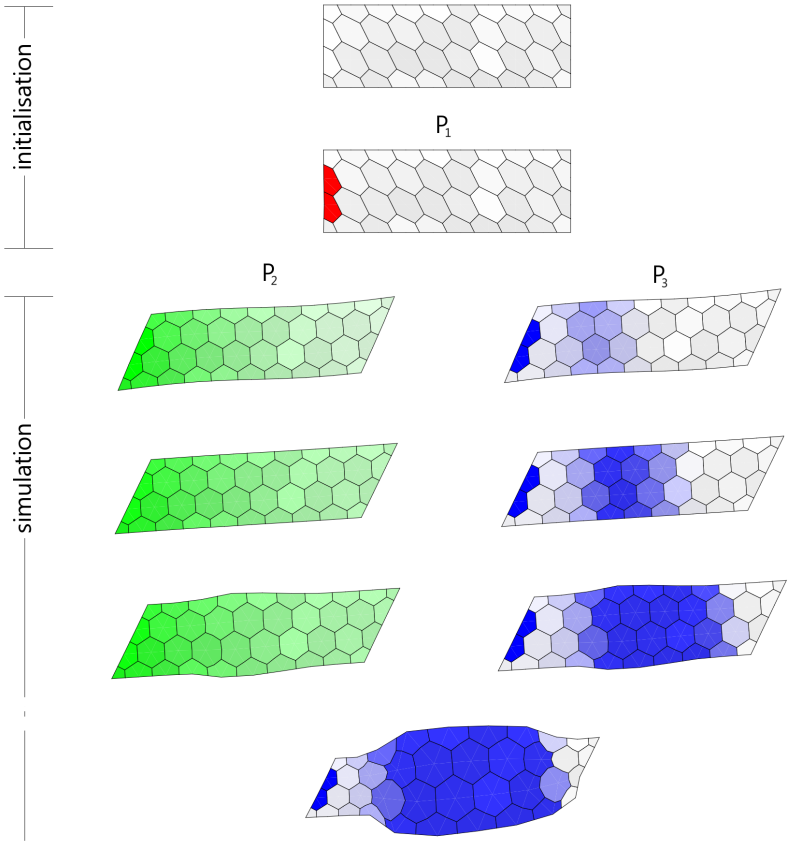


Figure 34: A simulation of simple drosophila-like segmentation. The diagram shows the cellular complex (as voronoi regions of the simplicial complex) with protein levels represented by the shading. The underlying simplicial complex is not visible in this image.

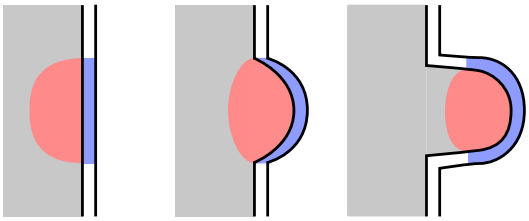


Figure 35: This figure demonstrates a simplified view of limb bud development: the mesenchyme (grey), the epithelium (lines), the AER (blue) and the PZ (red). The AER defines the PZ via diffusion of Fgf8. The PZ differentiates and releases Fgf10 which induces the AER to release more Fgf8. This feedback loop enables continual limb growth.

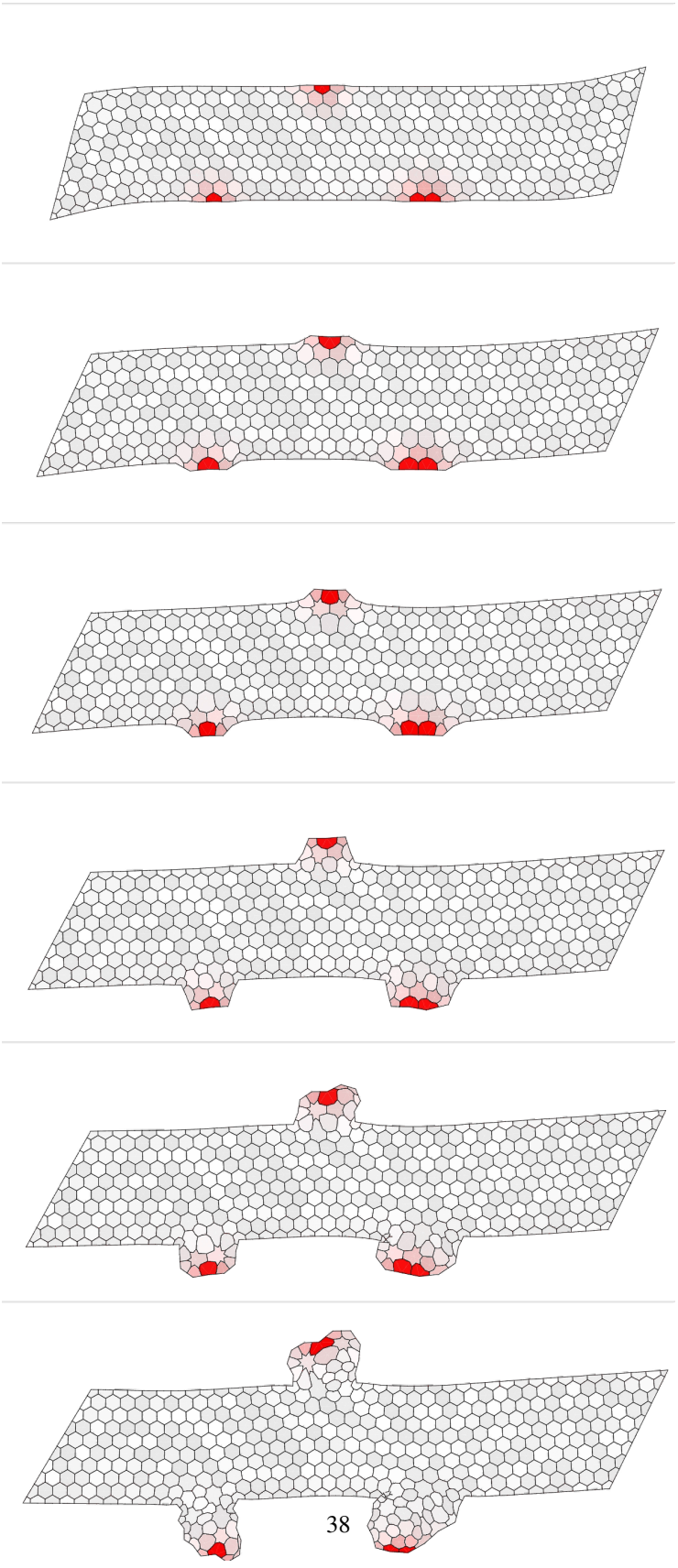


Figure 36: The formation of a protolimb in the developmental system from an initial state at the top then progressing in time downwards. The red region indicates level of protein Fgf8.

5.1 Structural

The cell operations have been designed for the 2D case and some hints given for the 3D case. The first important task that is to be done is to design the cell operations completely for the three dimensional developmental system. Some initial investigations suggest that these rules are not trivial as in the 2D case and hence we estimate **2–4 months** of research required to develop and implement these. A further **2 months** may be invested later into ensuring the rules are robust, clean, and simple. Other operations may be investigated according to the necessities of the biological models studied. Additionally, other facets of research include: balancing and maintaining a *clean* and smooth mesh and investigating adaptive behaviour.

5.2 Models of form

Research into biological models of developing systems constitutes a primary part of this research. Some preliminary research indicates that these models are generally easy to understand and implement, but difficult to abstract, control and reduce the parameters of. The goal is to study a particular property of form (e.g., segmentation), investigate the available biological models of it, then abstract, compare, and implement the models and illustrate how they can be used in a creative sense. Different models will be investigated, including: segmentation, phyllotaxis, limb growth, branching, spatial organisation, tropisms, and mechanical effects on growth, over a **12 month** period. An example set of forms will be grown that demonstrate these models, and illuminate the benefits of the developmental system.

5.3 Logical

The cellular programming part of the research will develop alongside the modelling part. Once the structural rules have been developed, some different cellular logic mechanisms will be investigated over a **2 month** period, focussing primarily on the connectionist and GRN methods. It is likely that the system will incorporate different aspects of different systems and be suited directly to the geometric aspects of SDS. The implementation of a robust framework for the chosen method or methods should take a period of no more than **2 months**. A method for isolating modules, combining different logics together, and using high-level constructs to define the logic may also be investigated, depending on time.

5.4 Physical

The protein signalling equations in three dimensions need to be elucidated and the framework implemented (**2 months**). The physical simulator is a non-trivial component of the system, and it is highly likely that the aggregate of developmental actions will have an unstable effect on the system, which could require up to **2 months** of work to alleviate.

5.5 Summary

The estimates above are quite lenient and the total (of **24 months**) does not reflect the simultaneity of the tasks. The thesis required for the academic qualification is estimated to take up to **4 months** full time work to write with contributions made to it throughout

the next two years. A journal paper is also expected to be submitted at the start of the third year (January, 2009). The following table summarises some key dates.

Date	Milestone
July, 2008	Complete 3D structural operations
August, 2008	Get married
October, 2008	Complete 3D implementation
January, 2009	Have working demonstrations. Submit paper to SIGGRAPH
March, 2009	Have a useful methodology for building shapes
May, 2009	Finish usable implementation
August, 2009	First thesis draft. Explore some other issues.
March, 2010	*Submit thesis*

5.6 Thesis Outline

This research will be presented in a thesis upon completion. A proposed outline follows.

1. Introduction
2. Literature Review
3. A Developmental System for Modelling Organic Form
   (a) Simplicial Complex and Transformational Operations
   (b) Cellular Communication and Organisation
   (c) The Genome
   (d) Physical Simulation and Environmental Aspects
   (e) Implementation Issues
4. How To Grow A Shape
   (a) Biology to the Abstract
   (b) Methodology
   (c) Segmentation
   (d) Phyllotaxis
   (e) Allometry
   (f) Radial Symmetry, *etc.*
   (g) Combining Multiple Properties
   (h) Some Complex Examples
5. The Artificial Embryo (outline of the software)
6. Conclusions and Discussion

5.7 Further research questions

There are numerous interesting research questions that arise from this work that inform possible alternate directions of research. These include questions of a theoretical, applied, and miscellaneous nature.

Theoretical

- What are the form generating capabilities of abstract mechanisms from embryogenesis? How expressive are some features (like protein signalling, RBNs, cell death, etc?)
- Can we apply them appropriately? Are there better methods than simulation?
- Changes in topology occur during development (for example, gastrulation). Can this integrate well into the system?
- Large cells are *representative* of an aggregrate of cells. Are there methods for defining aggregate behaviours well? E.g., allometric growth.

Applied

- Is simulation useful in a creative context? Can this approach integrate well with current methods? What tools/features do we need in order to interface them?
- Can simulation efficiency be improved? Can we get a *preview* of a program without running and simulating it completely?
- Are non-biological mechanisms useful?
- Is a genome that requires external input during development useful in the creative sense? Some examples are:
  - A genome that asks the user at every cell division whether or not the division should proceed.
  - A genome that reads in data from an input device (e.g., a microphone) and modifies activation thresholds accordingly.
  - A genome that requires morphogenetic gradients to be set up in the environment by the user during development, to e.g., grow a tentacle along a specific path.
- Higher level mechanisms. Can we abstract parts of genomes into *components*? And how would they combine? A library could then be built that has things like **segments**, **limb**, **phyllotaxis**, **thorns**, **eye**, *etc.*
- Could models be evolved? Given a specific creature, a user could be presented with various mutations and search the genome space via aesthetic selection.

Other

- Can this research apply to other domains? E.g., swarm robotics, replicating machines, *etc.*
- Could a *neurocontroller*, *sensor* and *effector* model be incorporated into the system, in order to design and build artificially alive organisms.

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