MATHEMATICAL MODELS FOR CELLULAR ORGANISMS

by

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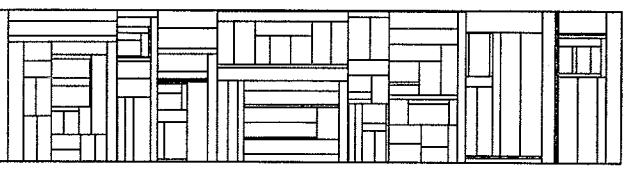
DATALOGISK AFDELING



INTRODUCTION

During the life of a cellular organism, the individual cells grow, divide and die. Our aim in this paper is to examine various mathematical models that represent this process as a sequence of discrete events.

In section I and II we give models in which the development of a cell is not affected by the spatial arrangement of the neighbouring cells. In section III we drop this restriction for one-dimensional organisms to get the Lindenmayer model [4]. The models in the remaining sections represent attempts to generalise the Lindenmayer model to higher dimensions. The Von-Neumann cellular array model of section IV proves unsatisfactory. The geographical models of section V, VI and VII are somewhat better for higher dimensional organisms. The final section gives a precise definition of a class of models, that includes those models presented earlier in the paper. The hope is that biologists will find these models suitable for discribing real organisms and that mathematicians will be stimulated to prove biologically interesting theorems about them.

I. GRAPH MODELS

Let us focus on the biological phenomen of cell division and death. In figure 1, we give a pictorial and graphical representation of the development of an imaginary cellular organism. How can we represent this development by a mathematical model? Suppose we have a set N of cell names. We can represent a stage in the life of an organism by giving for each cell in this life stage, its name and the names of its neighbours. The representation of the next stage in the life of the organism is then produced by:

1. using local transformation rules to convert each cell into a latent organism;

2. using an embedding rule to combine these latent organisms.

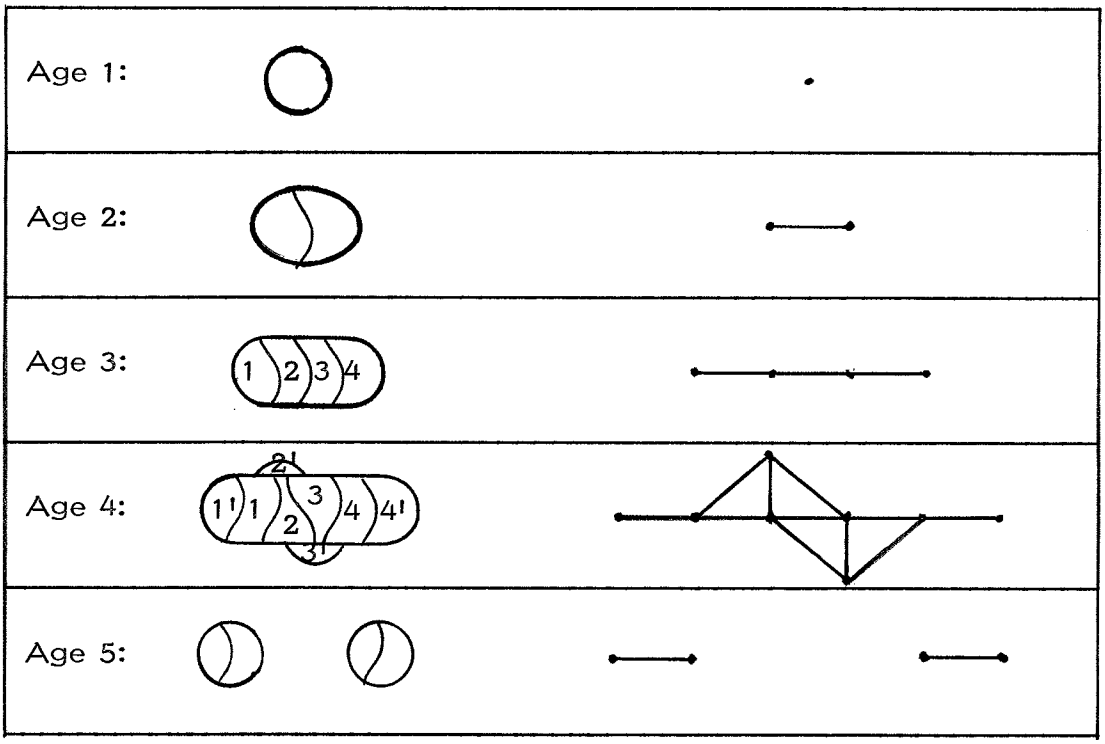


Fig. 1
The normal development of an imaginary organism

In figure 2. we show the local transformation rules used in our imaginary organism.

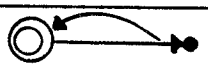
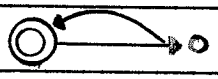
Name of rule	Condition	Latent organism
SPLIT	0, 1 neighbours	
THORN	2 neighbours	
DEATH	more than 2 neighbours	doesn't exist
STABLE	none	

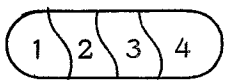
Fig. 2

Some local transformation rules for graph models

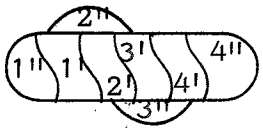
We note that latent organisms are graphs in which the vertices are divided into strong border cells (double rings), weak border cells (single rings) and interior cells (points). The reason for this vertex division is so that we can formulate the graph model embedding rule:

> Give distinct cell names to the vertices of the latent organisms. If an edge in the latent organism goes from cell i to cell j then j is a neighbour of i . If i is an interior cell, then it has no other neighbours. For border cells we must look at the neighbours of the cell which produced them. For a strong (weak) border cell the neighbours also include the (strong) border cells of the neighbouring latent organisms.

This sounds intricate but figure 3 should make it intelligible.



Cell name	1	2	3	4
Neighbours	2	1, 3	2, 4	3
Rule	SPLIT	THORN	THORN	SPLIT
Latent organism	 1′ 1″	2′ 2″	3′ 3″	4′ 4″



Cell name	1′	1″	2′	2″	3′	3″	4′	4″
Neighbours	1″ 2′ 2″	1′	2″ 1′ 3′ 3″	2′ 1′ 3′	3″ 4′ 2′ 2″	3′ 4′ 2′	4″ 3′ 3″	4′

Fig. 3

One epoch in the life of an imaginary organism

We have yet to explain the condition on the local transformation rules. This expresses a requirement on a cell and its neighbours. If we can map each cell into a rule in such a way that all these requirements are met, then the result of the process we have described is said to be a normal life stage. Sometimes it is convenient to make further distinctions between life stages: e. g. arrested life stage if the local transformation rule STABLE is used.

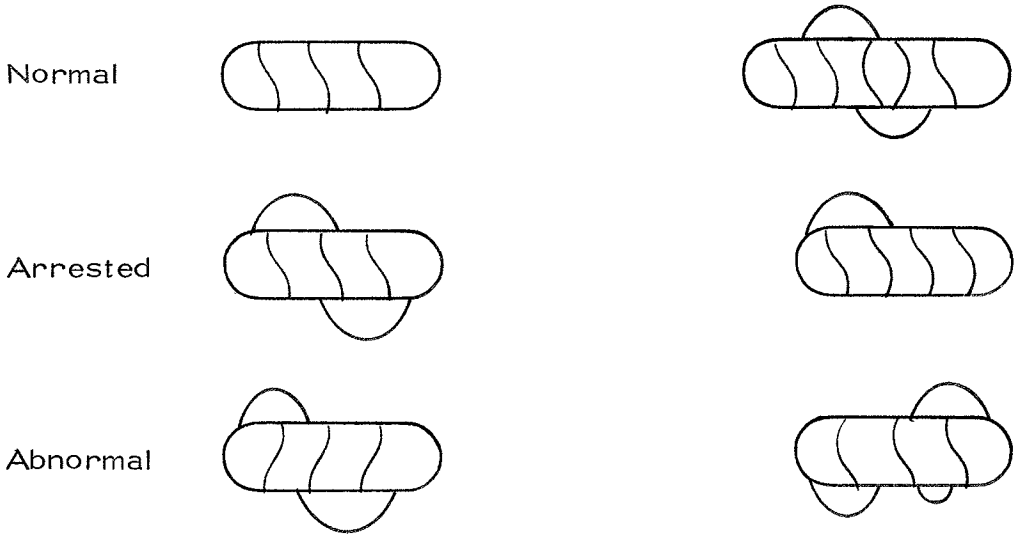


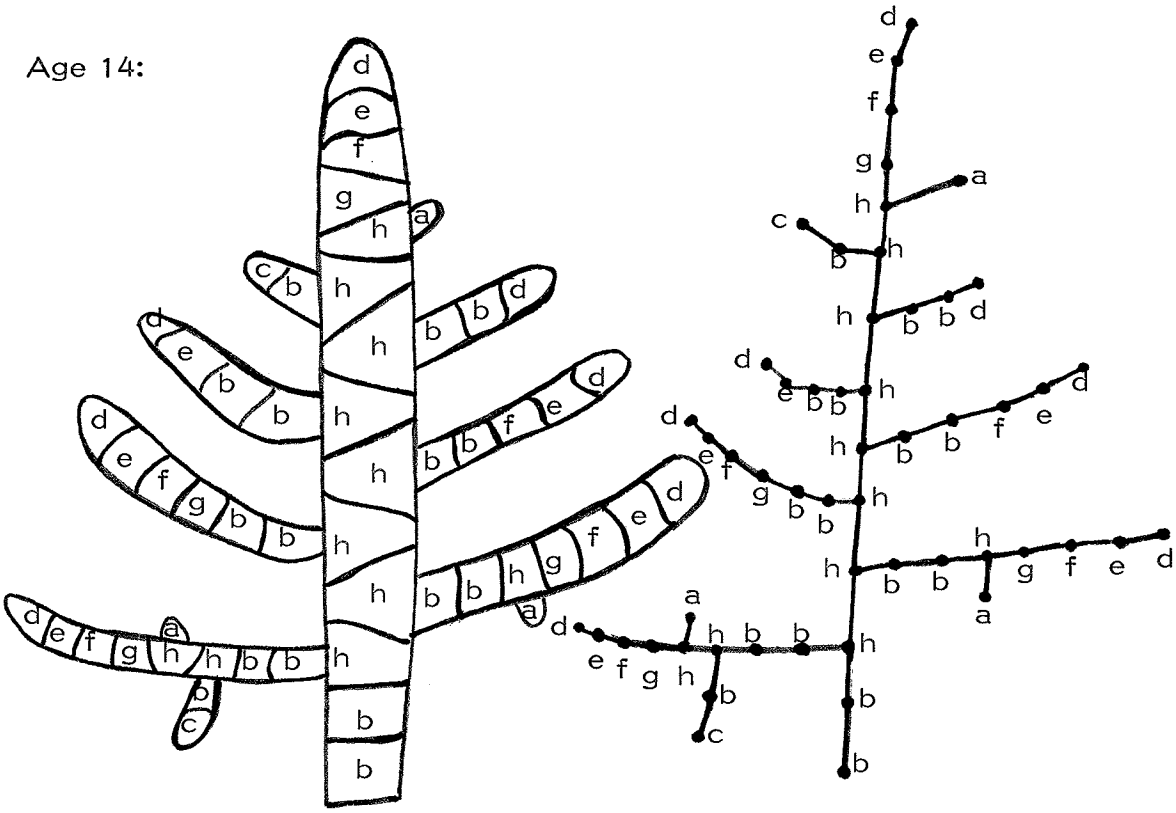
Fig. 4

Possible stages in the life of an imaginary organism

At last we can give a precise description of the growth of an organism. We define a grammar Γ to be a finite collection of local transformation rules and seeds (initial life stages). The language generated by Γ is the set of normal life stages that can be grown from a seed by repeated use of the process we have described above applied to normal life stages. For our imaginary organism the appropriate grammar is (SPLIT, THORN, DEATH, cell with neighbours). If we were also interested in arrested life stages, we could add rule STABLE to this grammar. Indeed there is nothing to stop us assigning probabilities to the various rules and studying the resulting destribution of life stages at different points of time. This can be done for each of the models in this paper and it is likely that the existing theory of stochastic automata [7] would give biologically interesting results. However we shall not discuss this possibility further.

II. WEB MODELS

It is not unnatural to suppose that the behaviour of a cell is dependent on its age and chemical constituents. Let T be a set of cell types. We must extend our mathematical model of a life stage in an organism by requiring an assignment of a type to each of its cells. This extension increases the range of organisms that can be modelled, because the conditions in a local transformation rule can now use type information about a cell and its neighbours. Figure 5 gives an example that is common in the literature.



Condition	a	b	c	d	e	f	g	h
Latent organism	b, c	b	b, d	e, d	f	g	h, a	h

Fig. 5

A model of Callithomnion roseum

Our model is now very close to the theory of web grammars [5] developed by computer scientists interested in pattern recognition. Web grammars are like Chomsky grammars in that they have auxiliary symbols and no parallelism, but even so their theory may prove biologicially relevant.

III. LINDENMAYER MODELS

Consider a one-dimensional organism in which an internal cell can divide. Our web model is inadequate, if the state of daughter cells depends on their order. Even if the context does not effect the particular states taken up by the daughter cell (0-L systems), it does affect their order. The new extension to our mathematical model of a life stage is: not only must one give the names of the neighbours for each cell, one must also say which of them is the left neighbour and which is the right neighbour. With this extension we have still more freedom in expressing conditions in local transformation rules. However we need a new kind of latent organism and a new embedding rule. A latent organism is a non-empty word on T. The embedding rule becomes:

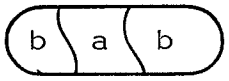
> Give distinct cell names to the letters in the words of the latent organism. Join these words according to the ordering of the original cell-first (last) letters of latent organisms usually acquire left-(right) neighbours and become right (left) neighbours. We now have a long word from which one can read off the left- and right neighbours of each cell.

In figure 6 we show an organism that can be simulated by a Lindenmayer model but not by the models we have presented hitherto.

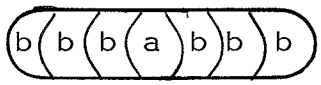
Grammar: seed (a) rules

name	condition	latent organism
A	type a	b a b
B	type b	b b

Fig. 6
(cont.)

Age 1: 

Cell name	1	2	3
Neighbours	$\langle\infty, 2\rangle$	$\langle 1, 3\rangle$	$\langle 2,\infty\rangle$
Rule	B	A	B
Latent org.	b b	b a b	b b
Neighbour representation	$1'$ $1''$ $\langle\infty, 1''\rangle\langle 1',\infty\rangle$	$2'$ $2''$ $2'''$ $\langle\infty, 2''\rangle\langle 2', 2'''\rangle\langle 2'',\infty\rangle$	$3'$ $3''$ $\langle\infty, 3''\rangle\langle 3',\infty\rangle$

Age 2: 

Cell name	$1'$	$1''$	$2'$	$2''$	$2'''$	$3'$	$3''$
Neighbours	$\langle\infty, 1''\rangle$	$\langle 1', 2'\rangle$	$\langle 1'', 2''\rangle$	$\langle 2', 2'''\rangle$	$\langle 2'', 3'\rangle$	$\langle 2''', 3''\rangle$	$\langle 3',\infty\rangle$

Fig. 6
A simple Lindenmayer model

We have chosen to present Lindenmayer systems in a form that can be generalized to higher dimensions. The price is that the presentation is somewhat more complicated than that in the extensive literature on one-dimensional systems [3]. This literature pays particular attention to the degree to which context influences local transition rules (the distinction between 0-L 1-L and 2-L systems) and contains many interesting results.

IV. ARRAY MODELS

How can the model of the last section be extended to dimensions higher than one? Even although the von Neumann cellular automata are not satisfactory because they cannot handle cell division, they have been used to model biological phenomena. Furthermore they may provide insight into the properties of more general models, because their theory is well developed [1].

The array model resembles the Lindenmayer model in that each cell in an organism has a fixed number of neighbours in a distinguished order. It is simpler than the Lindenmayer model in that the latent organisms are restricted to being a single cell of some type. This can be seen from figure 7 which gives an example that Conway has called LIFE-reputedly for antitheological reasons [2]. We have chosen LIFE because it cannot be simulated by a graph grammar in spite of the fact that the rules do not use the order of a cell's neighbours. If the reader computes one more step in figure 7, he will see that this is because separate organisms can move about and even combine. Indeed this possibility can be exploited to such a degree that Vitanyi has been able to design a cellular model that simulates the whole process of sexual reproduction [10].

Rules:

Name	Condition	Latent organism
LONELY	Type x and less than 2 x-neighbours	0
THRIVES	Type x and 2 or 3 x-neighbours	x
SQUASHED	Type x and more than 3 x-neighbours	0
BIRTH	Type 0 and precisely 3 x-neighbours	x
STABLE	Type 0 and not 3 x-neighbours	0

Fig. 7
(cont.)

Transformation:

Cell name	<1, 1>	<1, 2>	<1, 3>	<2, 1>	<2, 2>	<2, 3>	<0, 2>	<3, 1>	<3, 2>	<3, 3>
x-neighb.	3	5	3	5	6	5	3	3	3	3
Rule	T	SQ	T	SQ	SQ	SQ	B	B	T	B
Latent org.	x	0	x	0	0	0	x	x	x	x

Fig. 7
A cellular model

In the theory of (cellular) array models one usually requires that cells can have a type that is quiescent in the next sense that a cell does not change from this type if all of its neighbours also have this type. With this requirement organisms can only grow by extending their skins over quiescent cells.

In our earlier models latent organisms also had skins: border cells in graph and web models, left and right ends of words in Lindenmayer models. Why did we need such a skin ? In order to formulate the embedding rule for the model, and thereby to specify precisely a new life stage of an organism in terms of a previous life stage and the development of its individual cells.

V. MAP MODELS

Consider a map of continental Europe. How would this change if France should suffer a revolution and be divided into two parts? The point to note is that Germany and Italy cannot be neighbours of the same part unless this part also has either Spain or Switzerland as a neighbour. Rosenfeld and Strong [8] have formulated this restriction in terms of n-multigraphs graphs whose edges are cyclically ordered at each vertex. However J. Thatcher has suggested that the restriction be formulated in terms of a function from an alphabet into words on the alphabet. This prompts the introduction of circular words on an alphabet S as ordinary words on S with:

1. a clockwise or anticlockwise orientation;

2. the understanding that the first (last) letter is the right (left) neighbour of the last (first) letter.

The context of France, its neighbours in their precise ordering, is given by a circular word on country names. The contexts of the parts of France after the revolution must be subwords of the context of France.

Before returning to biology it is instructive to extend the geographical example further by supposing that countries do not divide arbitrarily. Suppose all revolutions are due to religion, that a revolution only arises in a state if two of its neighbours have differing religions, and that the state divides in such a way that each part has a co-religionist as a neighbour. Then the division of the context of the state depends on the religions of its neighbours.

Now consider the arrangement of cells in a leaf. Figure 8 uses circular words to give a mathematical model of such a cell arrangement. [Nägeli 6]. We also use the convention that the orientation of clockwise circular words is not shown and leave the mathematical reader to discover why orientations are not needed here and elsewhere in this section.

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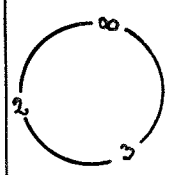
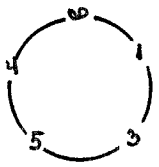
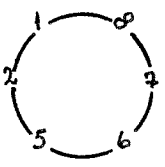
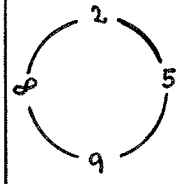
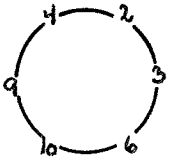
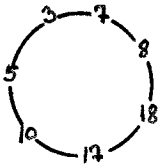
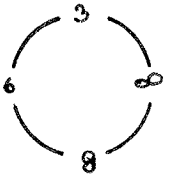
**)							
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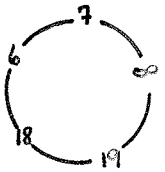
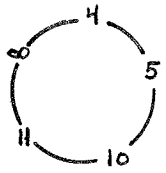
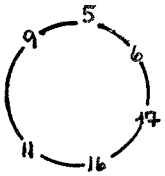
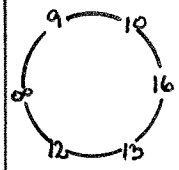
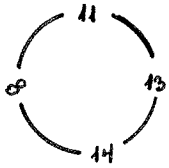
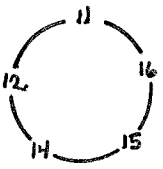
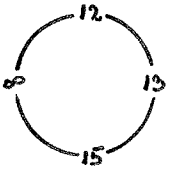
**)							
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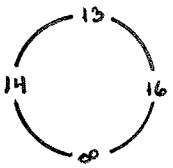
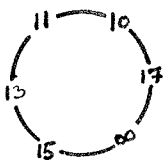
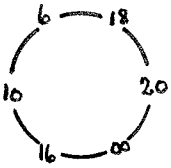
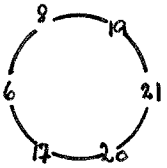
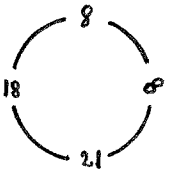
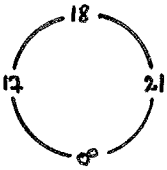
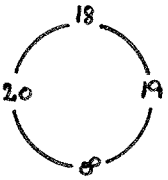
**)							

*) Cell name

**) Context

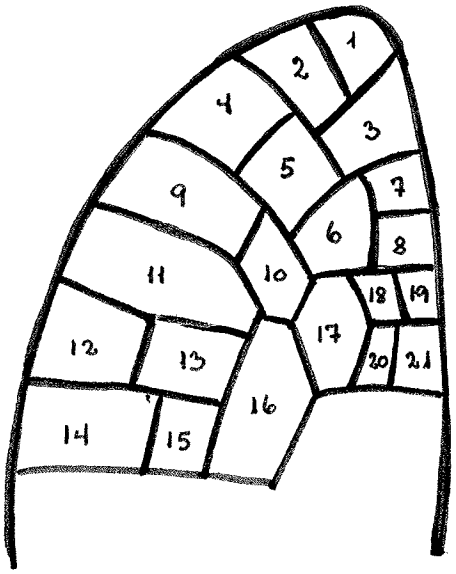


Fig. 8

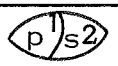
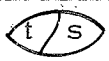
Representation of a leaf

Now we can present the map model of the life stage of an organism. It consists of a finite set of cells, each with a name , a type and a context. A context is a circular word on the cell names. The latent organisms consist of:

1. a finite set of cells, each with a name, a type and a context;
2. a circular word on the cell names, the skin;
3. a restriction on the way the latent organism can be embedded (religions in our geographical analogy).

We get the skin of a latent organism by running along its outside edge and reading off the names of the cells we truck. The restriction limits the way the skin can be broken into subwords in the embedding process. Before plunging into the details of this process, let us look at the rules for the leaf of Phascum Cuspidatum. In figure 9 we have cheated a little by using a picture instead of giving the latent organisms in the form required by 1. and 2.

Rules:

Name	Condition	Latent organism
BUD	Primary cell	 Division touches ∞
ANTI	Secondary cell	 Division touches ∞
PERI	Secondary cell	 s touchs ∞
STABLE	Tertiary cell	 NONE

Seed:  cell type: p cell context 

Fig. 9

The map grammar for Phascum Cuspidatum

The reader should consult figure 10, 11, while we give the details of the embedding rule for the map model. Suppose we have a collection of latent organisms, one for each cell in the current life stage. The first step is to modify the context of the skin of one of the latent organisms using the context C of the corresponding cell. We do this by splitting C into ordinary words, one for each skin cell, then substituting these ordinary words for occurrences of ∞ in the skin cell contexts. In splitting C, we must pay attention to the restriction associated with the latent organism. Having split C, we are ready for the second step - of substituting ordinary words on skin names for occurrences of c in the context of neighbours of c. We repeat this process for each latent organism in turn.

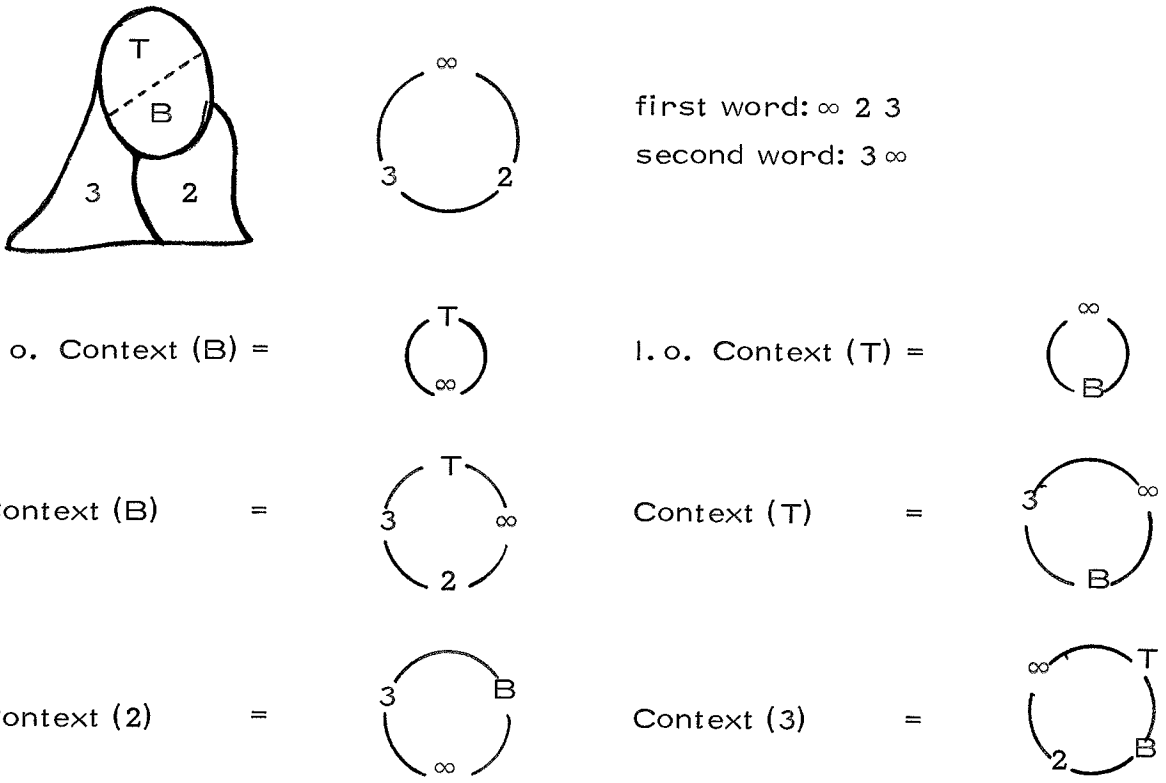
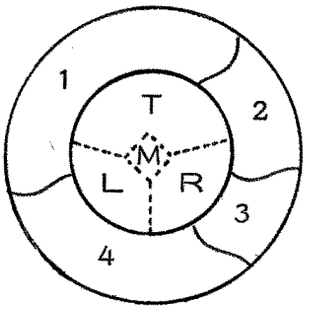
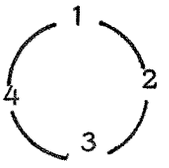


Fig. 10
Splitting and joining



cell context:



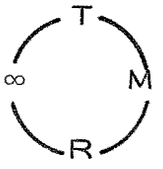
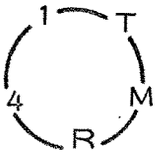
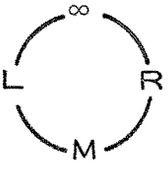
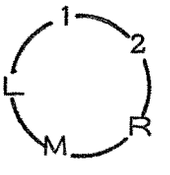
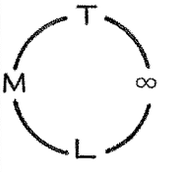
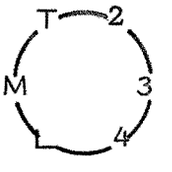
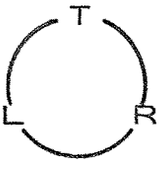
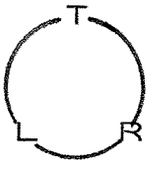
Name	Word	l.o. context	Context
L	4 1		
T	1 2		
R	2 3 4		
M	-		

Fig. 11
(cont.)

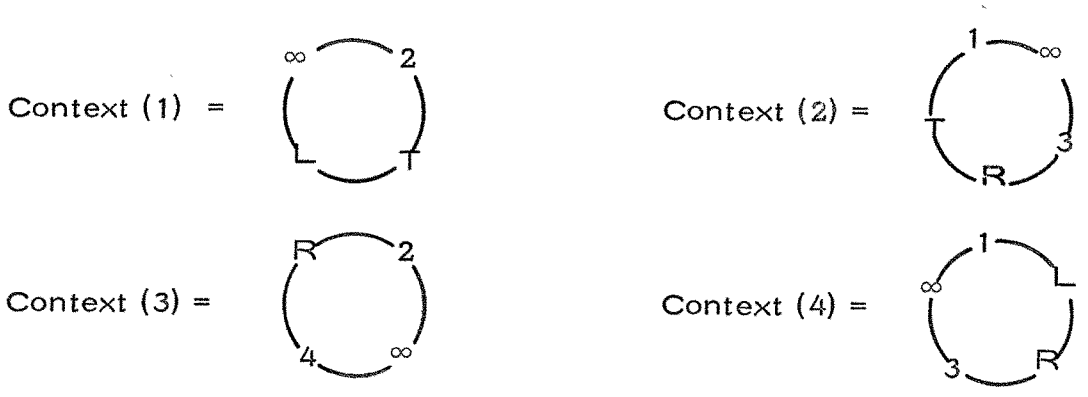
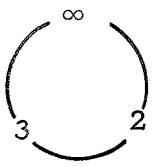
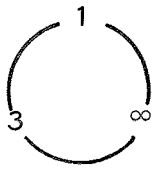
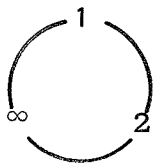
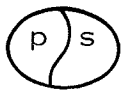
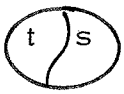
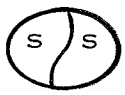
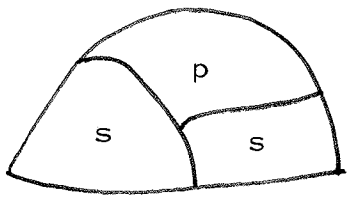


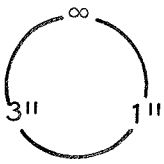
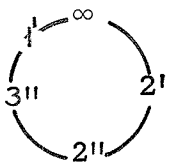
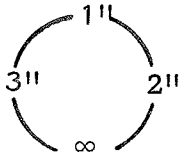
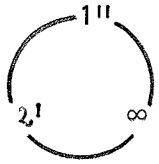
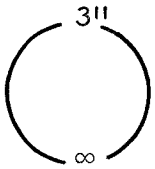
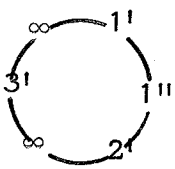
Fig. 11
Disintegration and rejoining

For a more complicated example we can take a life step in the organism whose grammar is given in figure 9.

We note that the embedding restriction on the latent organisms are satisfied in figure 12; ∞ divides the words for the context of cells to which we applied BUD and ANTI, ∞ is in the second word for the context of the cell to which we applied PERI.

Cell Name	1	2	3
Context			
Rule	BUD	PERI	ANTI
Latent organism			
Context words	3 ∞ , ∞ 2 3	∞ 3 1 , 1 ∞	∞ , ∞ 1 2 ∞



Name	1'	1''	2'	2''
Context				
Name	3'	3''		
Context				

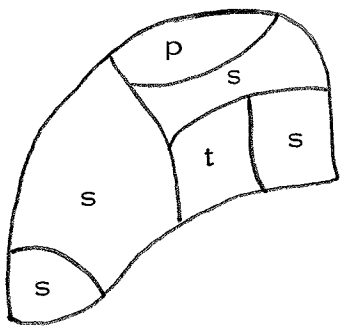


Fig. 12
An epoch in the life of a Phascum Cuspidatum leaf

In our last example we have a case of multiple touching: cell 3'' has two occurrences of the environment in its context. Paying due attention to the fact that the order of occurrences of a in the context of b is the reverse of the order of occurrences of b in context of a, this can be unravelled mathematically.

However there is another interesting solution: to suppose our circular words have a pointer like the hand of a clock. The embedding rule would have to be changed but the alterations are slight. Having made the changes, one can mention the pointer in the conditions of the transformation rules. One possibility would be to make the rules dependent on the direction of the light falling on the organism.

VI. ISLAND MODELS

Before eggs and other 3-dimensional organisms can be modelled, we must generalize our map model to allow islands. How can we use circular words to describe the relation of England to the rest of Europe? The answer is to use more than one circular word to describe the context of the sea. An example which looks more biological is given in figure 13.

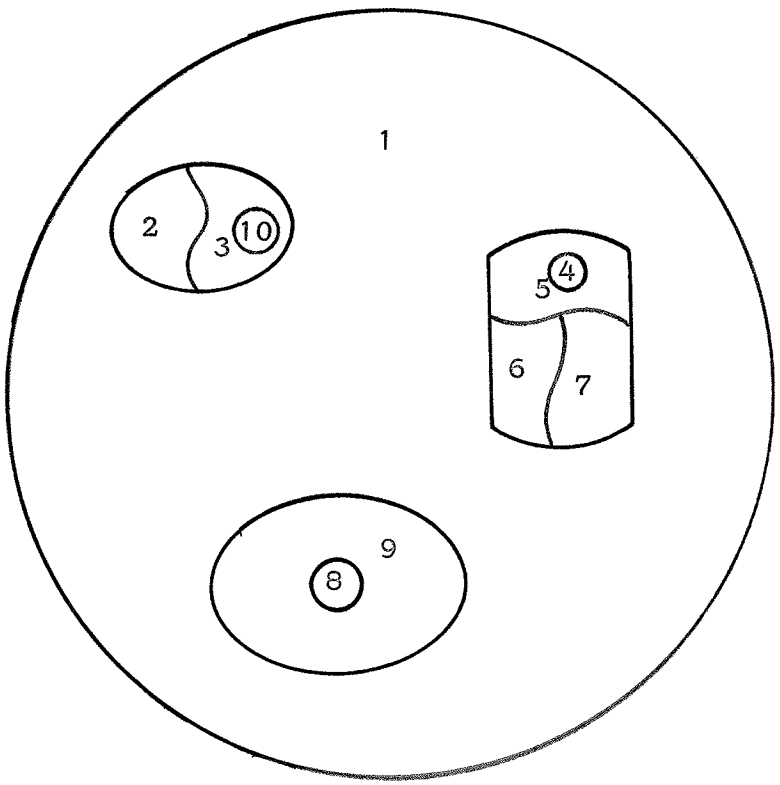


Fig. 13
(cont.)

Cell name	Context			
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				

Fig. 13

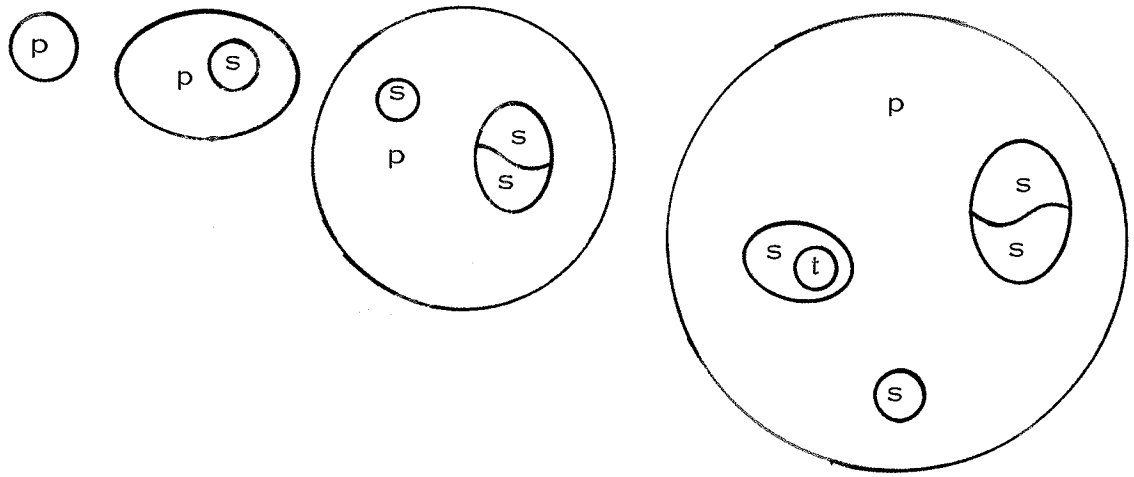
Internal components of an organism

The description of cell division in the last section (figure 11) must be modified to allow for the presence of islands. If we assume that the line of division never splits an island, this modification is easy:

> Islands can be distributed arbitrarily between the daughter cells.

If the line of division is allowed to pass through an island, the modification of the cell division rule is not so easily formulated. A related problem is that of islands, that disintegrate into several islands. At the end of the next section we shall indicate how these problems can be treated. Here we shall only describe how the formation of an island affects the context of a cell. If an island m is formed in a region n then n adds the counter clockwise circular word m to its context, and m takes the clockwise circular word n as its context. Figure 14 should make this clear.

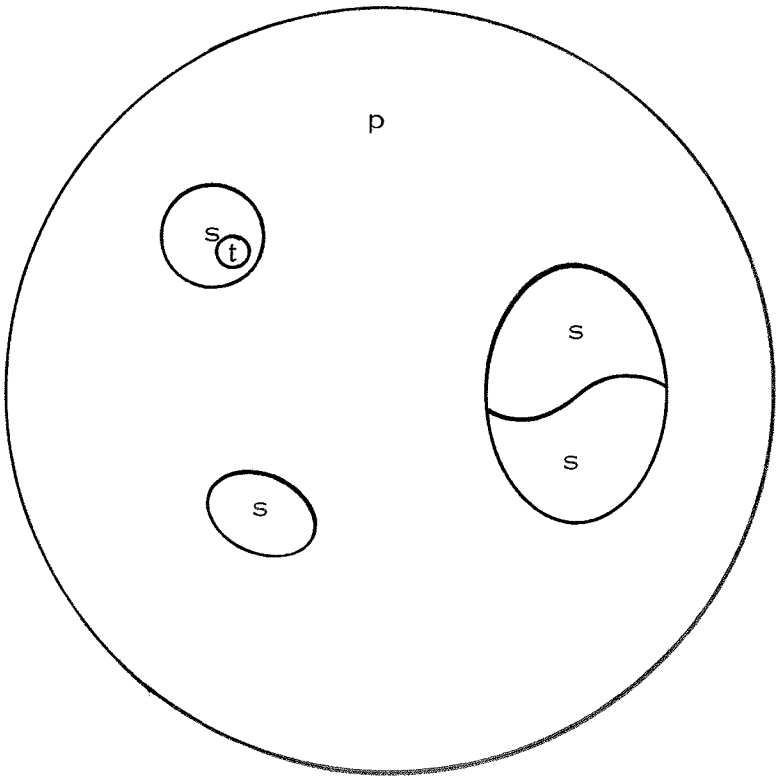
Life history:



Rules:

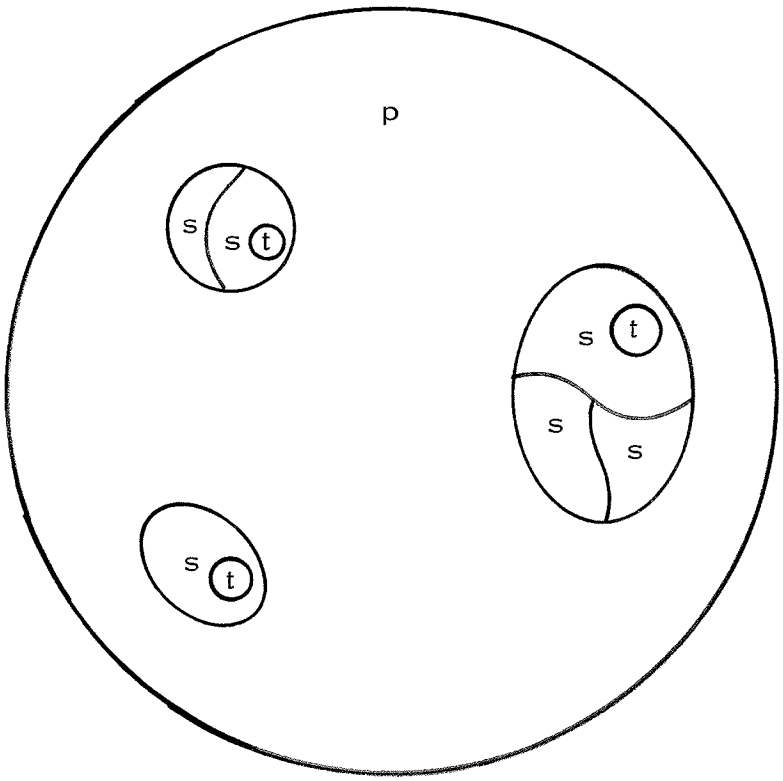
Name	Condition	Latent Organism
BABY	Primary	s p
SPLIT	Secondary	△ s s ▽
HOLE	Secondary	s t
STABLE	None	●

Fig. 14
(cont.)



Cell name	1	2	4	6	8	10
Context	∞	1	1 6	1 4	1	2
	2 8	10				
	4 6					
Rule	STABLE	SPLIT	HOLE	SPLIT	HOLE	STABLE
Latent organism	●	s s	t s	s s	t s	●

Fig. 14
(cont.)

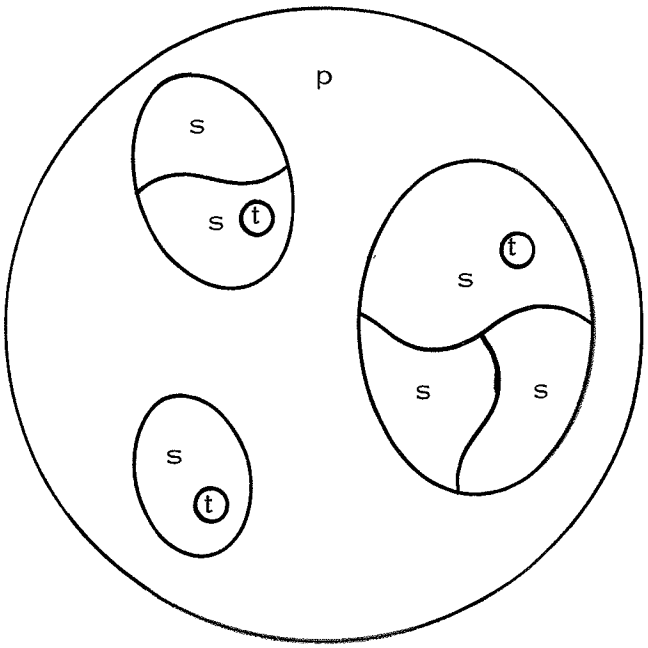


Cell name	1	2'	2''	4'	4''	6'	6''	8'	8''	10
Context	∞	1 2''	1 2'	1 6' 6''	4'	1 4' 6''	1 6' 4'	1	8'	2'
	2' 2''		10	4''				8''		
	8'									
	4' 6' 6''									

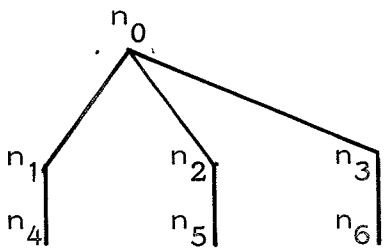
Fig. 14

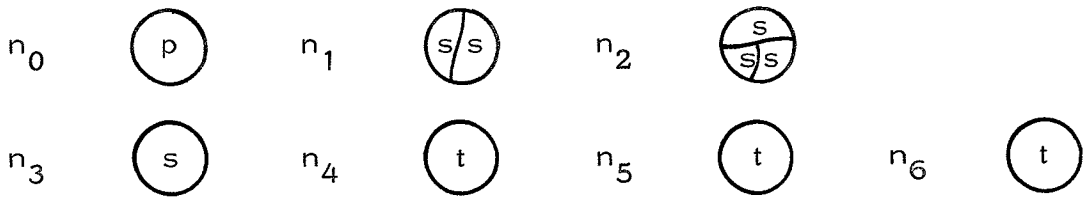
The development of internal organs

An island model can be represented as a labelled tree in two ways (figure 15). Either we can have a node for each island or we can have a node for each cell. In the former case the labels refer to map models and we do not see which cell an island belongs to; in the latter case the labels are states and we do not see the interconnection between regions. (See appendix). Nevertheless it seems likely that the existing theory of tree automata and grammars can profitably be applied to island models [9].



Island tree:





Cell tree:

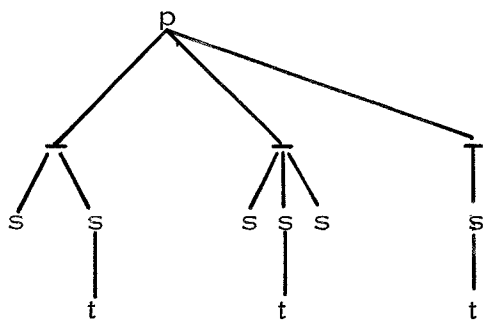


Fig. 15

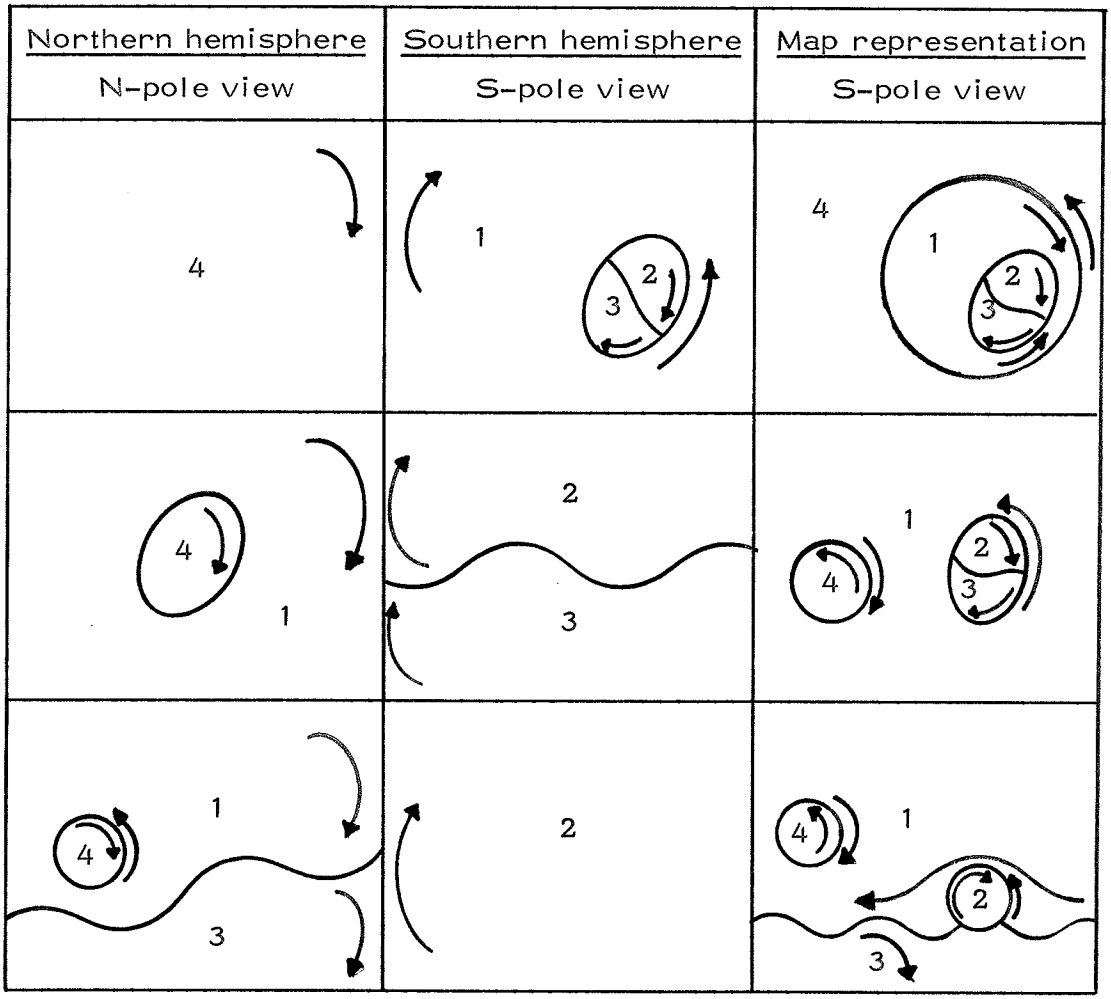
Tree representations of island models

VII. SPHERICAL MODELS

At last we can present a model for a 3-dimensional organism. First imagine a demon inside one of the cells of a two dimensional organism. It would see the outside world as a circle, which the neighbouring cells divide into segments. It could model this world using circular words. Now imagine a demon inside one of the cells of a three dimensional organism. It would see the outside world as a sphere, which the neighbouring cells divide into regions (contact areas, clouds). It could model this world using spherical words, if only we had a suitable definition of spherical words. But this has been given us by the last two sections, spherical words can be defined in terms of circular words.

How can we describe the way a spherical word divides into several spherical words? For simplicity we consider only division into two parts in what follows. Revive the two dimensional demon for a moment. It split a circular word into two ordinary words by picking two letters, then converted these back to circular words (see figure 10). In the discrete world of the model this corresponds to - splitting a circle into two lines by picking two points, then converting each line into a circle by adjoining a new line. The analogous process in three dimensions is - splitting a sphere into two hemispheres by picking a circle, then converting each hemisphere into a sphere by adjoining a new hemisphere. We have to make this precise in the discrete world of spherical words.

Let us define a <u>flat word</u> as a collection of circular words that represent a map. Figure 8 and 13 give examples of flat words but they are somewhat special because they have only one unbounded region. In any case the arrangement of the unbounded regions in a map can be described by one counterclockwise circular word, the <u>skin</u> of the corresponding flat word. Consider two flat words. They can be joined by rolling the skins over one another (ie. modifying the external context of the unbounded regions.)



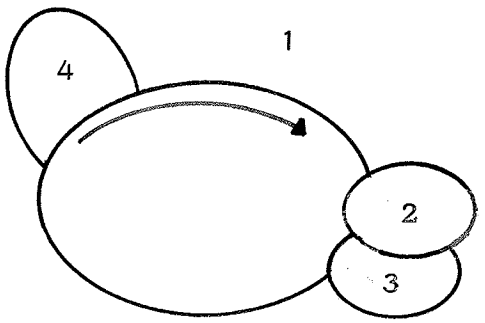


Fig. 16

The formation of a spherical word from two flat words

Three examples of the process of joining two flat words are given in figure 16. The last column gives a map representation of the result of the joining process under the convention: the northern hemisphere encloses the southern hemisphere, so the orientations of the northern hemisphere circular words are reversed (remember that eastward passage of the equator is clockwise from the south pole, anticlockwise from the northpole. With other conventions we get other map representations of the results. The important point is that in each example the results of joining the two flat words is the same spherical word, even although this spherical word has a multitude of map representations.

But how does a spherical word split into two flat words? What if we pick a simple closed curve in one of the map representations of the spherical word and let the inside and outside of the curve give us the two flat words? This will solve our problem if we can give a precise description without mentioning map representations.

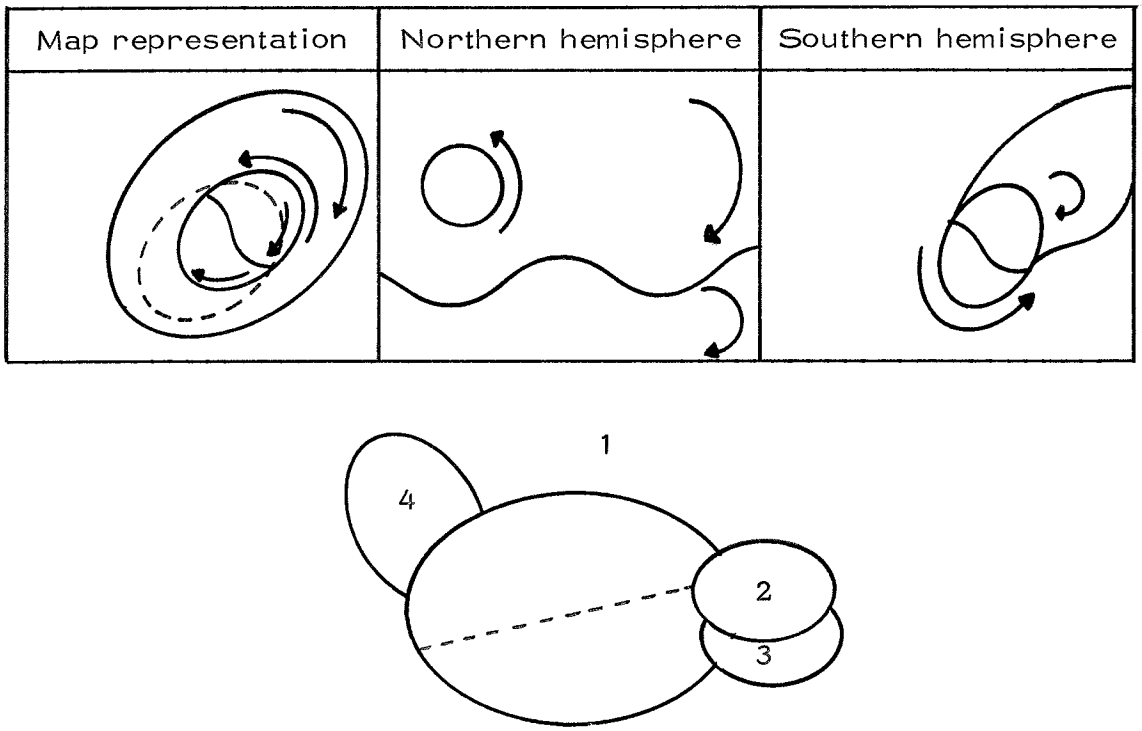


Fig. 17
The splitting of a spherical word 1

We can define a <u>thread</u> in a spherical word so that it corresponds to a simple closed curve on a sphere. A thread is a sequence of letters:

$$l_1, l_2, \ldots\ldots\ldots, l_n$$

such that $l_1 = l_n$ and for $i = 1, 2, \ldots\ldots, n$ we have

1. l_i occurs in the circular word that is the context of l_{i-1}

2. if $l_i = l_j$ then the circular word that is the context of l_i and the occurrences of l_{i-1} and l_{i+1} do not separate the occurrences of l_{j-1} and l_{j+1}.

Figure 18 should make this clearer, although it can not illustrate condition 2 because there is no circular word with more than three letters.

Thread for the split in figure 17:

1, 2, 1

Thread for a more complicated split:

1, 2, 1, 3, 2, 3, 1, 4, 1, 4, 1

A letter sequence that is not a thread:

1, 2, 3, 4, 1

Spherical word in figure 17

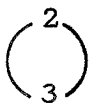
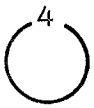
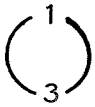
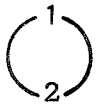
Cell name	Context	
1		
2		
3		
4		

Fig. 18
Threads and spherical word splitting

The time has now come when we can define the splitting of a cell c in a three dimensional organism. The process is:

1. pick a thread in the spherical word that is the context of c ;

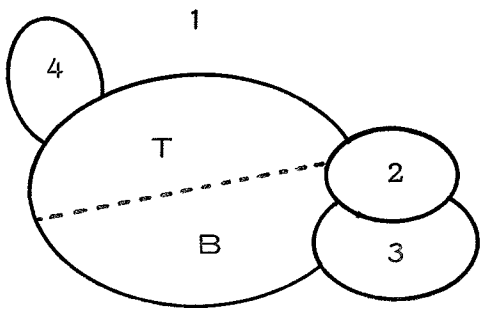
2. Use this thread to split the spherical word into two flat words;

3. Join one of these flat words with the flat word c' and take the resulting spherical word as the context of the daughter cell c'';

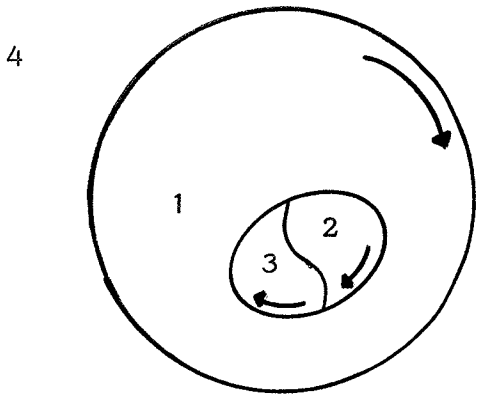
4. Join the other flat word with the flat word c'' and take the resulting spherical word as the context of the daughter cell c' ;

5. Replace c by c' or c'' in the context of the letters occurring in the two flat words but not in the thread;

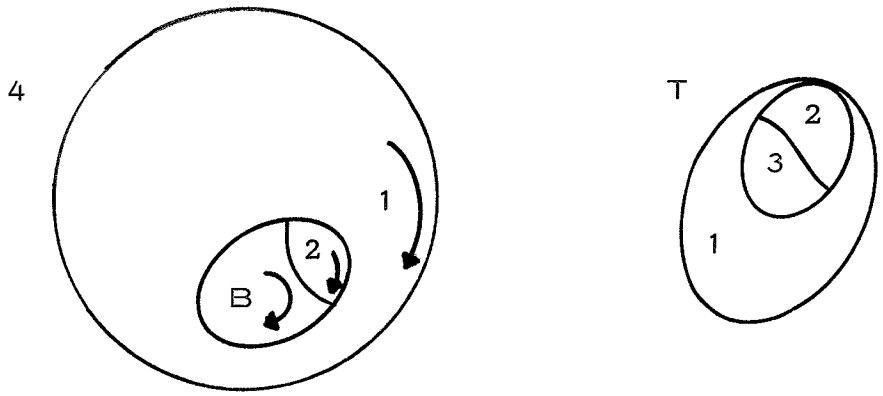
6. Replace c by $c'\,c''$ or $c''\,c'$ in the context of the letters occurring in the threads.



Original S-pole representation of the context of the dividing cell



Context of daughter cells



Context of other cells

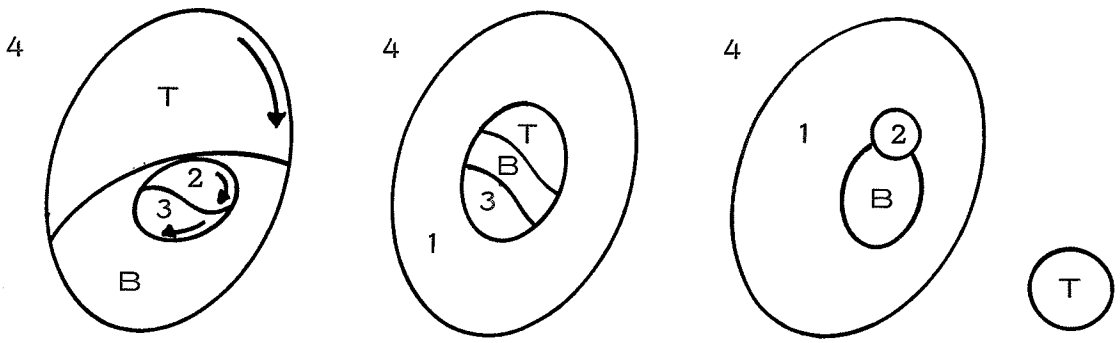


Fig. 19

The result of a 3-dimensional split

It is natural to ask for a three dimensional analogue of islands. The answer is immediate:

> a cell in a three dimensional organism can have more than one spherical word as its context.

We can allow rules by which a cell can become pregnant in that the rule adds a one letter spherical word to the context of the cell. The reader who has followed us this far will have no difficulty in filling in the details.

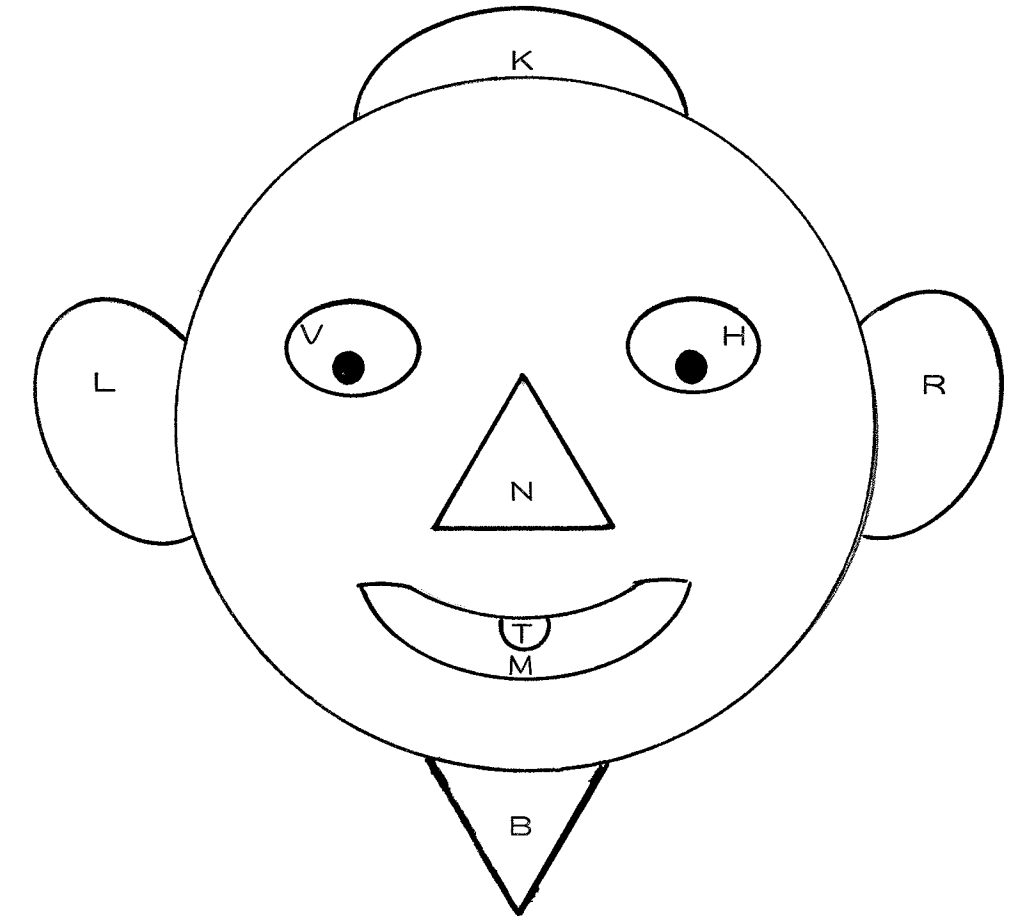
Let us conclude this section by pointing out that our concept of a thread may prove useful for two dimensional organisms. When such organisms have the environment as their only unbounded region, they may be considered as collections of spherical words. In this case our concept of a thread can be used to describe the modification of cell division in the case when the line of division passes through an island - the problem we left open in the last section.

VIII. THE GENERAL MODEL

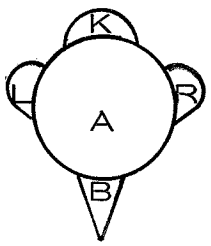
A life stage in an organism is represented by a finite set of cell names, a map τ from these cell names into a set of types, and a map γ from these cell names into a set of contexts. The development of an organism is modelled by a grammar which consists of a set of initial life stages and a set of local transformation rules. A transformation rule consists of a condition and a latent organism. The condition only refers to the result of applying the map τ to the context of a cell and the cell itself. A new life stage results if we can assign rules to the cells of a life stage in such a way that all conditions of the rule are met. The rules gives a latent organism for each cell and the embedding rule for the model tells how these latent organisms are combined into the new life stage. The embedding rule may well refer to the map γ of the life stage of the organism that is developing into a new life stage.

As the problem of generalizing the Lindenmayer model prompted this paper, let us close it with an indication that we have found the correct generalization. In topology a 2-sphere is a circle and a 1-sphere consists of two points. Here the context of a 1-dimensional cell is a two letter word, the context of a 2-dimensional cell is a circular word, and the context of a 3-dimensional cell is a spherical word. If the real world had a higher dimension, the appropriate Lindenmayer model would be at hand.

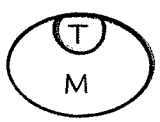
IX. APPENDIX



map a:



map b:



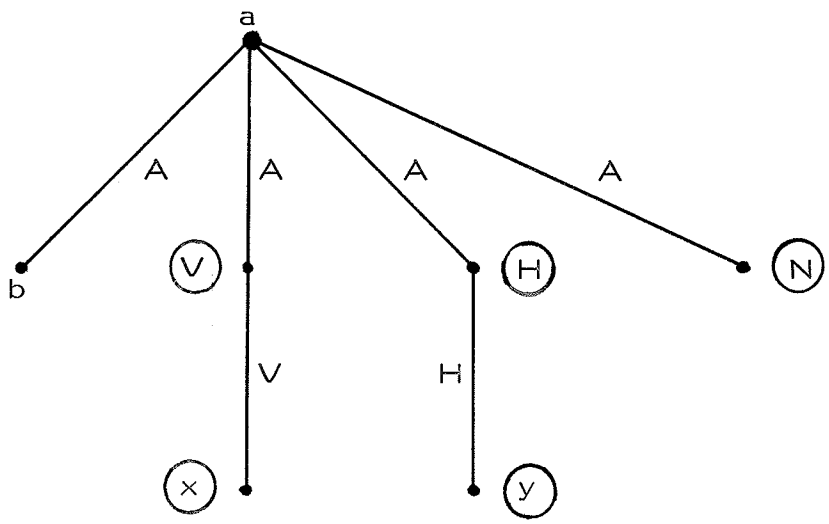


Fig. 20

A tree representation of an island model

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NB! We have a computer program that plots stages in the life of a twodimensional Lindenmayer System.