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## The simulation of branching patterns in modular organisms

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[Plate 1]

A modular mode of growth in an organism is frequently coupled to the development of a branched structure. Such modular forms may appear to be constructed in a regular manner, exhibiting a high degree of organization, or may be bewilderingly complex and yet not haphazard. These factors, together with the very nature of systems dependent upon the progressive addition of modules, readily promote attempts to model branching processes by means of some sort of constructional simulation. Such models tend to favour visual, graphic presentation. This paper considers aspects of modularity and branching and the different approaches to the modelling of branching organisms, and gives a range of examples. Attention is directed towards the aims of the models and to their different characteristics rather than to a description of the computer methodology involved. Attempts to simulate branching systems highlight the constructional similarities and differences between various modular organisms, but one key factor is identified for both real and artificial branching patterns: it is the nature of the control of new branch initiation that governs their constructional development.

### 1. MODULARITY

The recognition of some aspect of modular construction in diverse organisms is not a new concept. It has featured periodically in biological thought but this time its appearance has coincided with the advent of computer technology. The discrete events and entities of modular growth encourage investigation by means of computer simulation, endowed though they are with assumptions regarding ‘function’ and ‘efficiency’.

Modular assemblages develop most frequently into branching forms, and it is the interpretation of the organization behind such complex ‘trees’ that challenges the morphologist. Frank Lloyd Wright was intrigued by form in the context of his organic architectural designs, and his sentiments apply equally to branched organisms.

‘Realization of form is always geometrical. That is to say, it is mathematic. We call it pattern. Geometry is the obvious framework upon which nature works to keep her scale in “designing”. She relates things to each other and to the whole, while meantime she gives to your eye most subtle, mysterious and apparently spontaneous irregularities in effects.’ (Wright 1953)

The implication here is that there must be an intrinsic order to branched growth even in the most elaborate system. An understanding of this sequence demands recognition of the nature of the building blocks for a given type of organism: a ‘module’ of some kind.

The traditional botanical description of a branching system, the floral diagram, disguises or fails to appreciate the dynamic aspect of branching and its inherent modularity, although such diagrams do convey a great deal of information and can be aesthetically superb (Engler 1876)

(figure 1). Dynamic information is obtained if a time sequence of events is presented (for example, Darrow 1929; figure 2) and it is here that a modular approach can be identified. This qualitative manner of monitoring the developmental morphology of plants as they age is directly amenable to simulation model production. An example is seen in Tumidajowicz & Dambski (1984) where sequences of annual rhizome increments are represented as the structural components of a binary 'tree' to represent long term genet growth rather than detail of branching morphology *per se*. The analogy of a computer data structure in the form of a 'rooted tree' and the branching within real trees forms the basis of at least one computer model of tree crown development (Smith & Scoullar 1975).

An organic branching pattern develops by the addition of new components to an existing framework. Depending upon the nature of the organism, these components may be more or

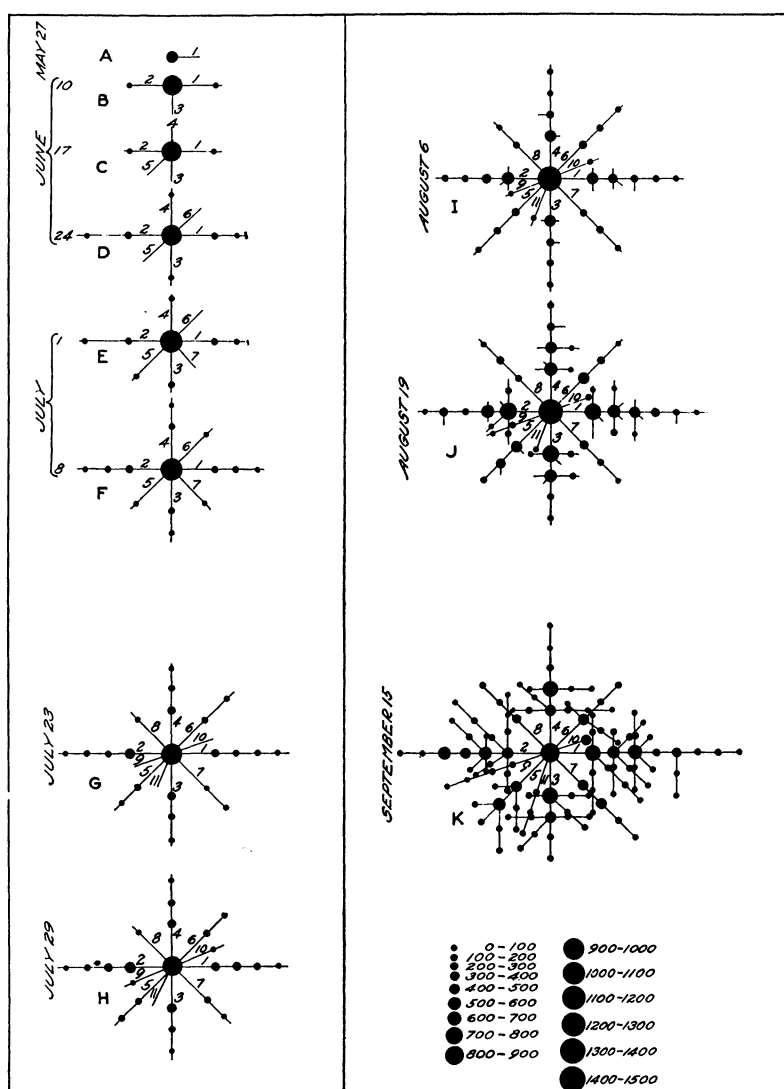


FIGURE 2. A process description of plant form showing a developmental sequence of runner production in strawberry (from Darrow (1929)). In zoological terminology, A represents the ancestrula and the sequence A-K the astogeny of this branching pattern.

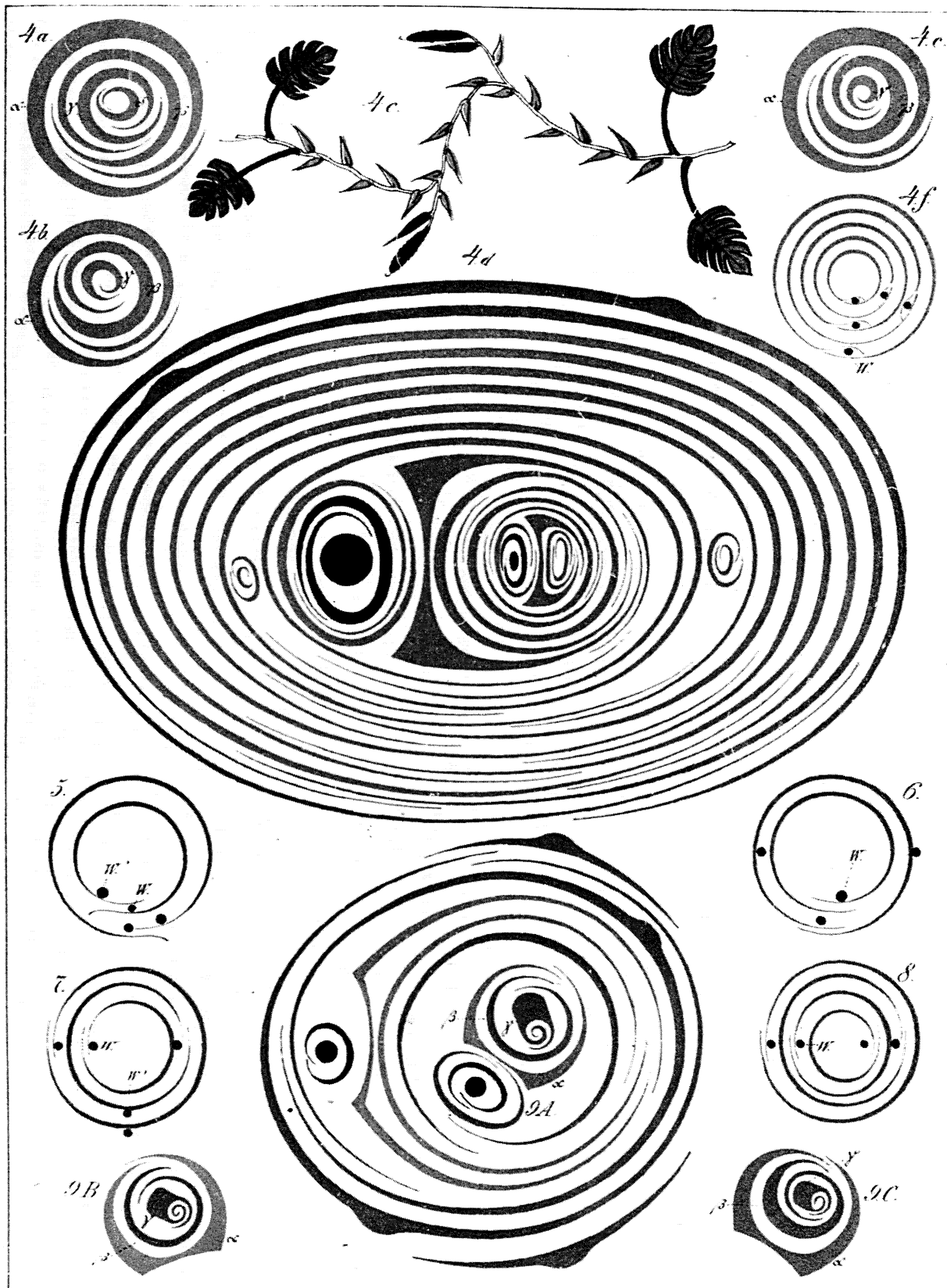


FIGURE 1. A 'floral' diagram. A traditional state description of plant form (from Engler (1876)).

(Facing p. 144)

less discrete and conform to a greater or lesser extent to one's personal notion of a module. Thus the definition of a modular unit presented by Finks (1973), relating to the uncertain construction of extinct calcareous sponges (Sphinctozoa), has to be deliberately vague: 'a structural unit which makes up, in the aggregate, a given individual or other entity'. Nevertheless an understanding of the development of an organism will help define its modular nature and determine the usefulness of the concept for a particular situation. In bryozoans the individual zooids of the colony readily lend themselves to the epithet 'module' and these modules are aggregated into a branching entity. In many cases, however, application of the modular concept is a matter for debate (outlined in Mackie 1963; White 1984). There is also a temptation, not necessarily fruitful, to look for levels of modular construction within one organism: 'logic can carry one to the conclusion that all colonies are individuals or that all individuals are colonies' (Boardman *et al.* 1973). This paradox may occur whenever modularity is used to analyse a construction. Even the design of complex computer systems involving numerous hardware and software components which can be rationalized by recourse to a modular approach can suffer this complication (Unger & Bidulock 1981).

Branched modular constructions are ubiquitous and, one must assume, successful modes of growth (Mackie 1963). Particularly throughout the plant kingdom, the advent of growth restricted to an apical region represents the morphological key to the branched habit, a potentially efficient mode of development if coupled to the related physiological imperatives of plant architecture (Raven 1984). Apical meristems create building blocks which, in turn, create structure. In the botanical field the soundest level at which to identify modules and their interactions, in my opinion, is that expounded by Prévost (1967) who defined a botanical module as the product of one apical meristem that has a definite, ultimate fate, such as the formation of a terminal inflorescence. The epicotylar meristem of sycamore (*Acer pseudoplatanus*) grows for many years and metres to constitute the trunk of the tree before revealing its determinate nature by terminating in a solitary flower (see also examples in Barthelemy, this symposium). Even the epicotylar meristem of a coconut palm (*Cocos nucifera*) or a monkey puzzle tree (*Araucaria* species) ceases to grow eventually. It is useful from a constructional point of view to recognize each such component, representing the product of a single meristem, as a module. Modules commonly form the components of a sympodial axis and are often determinate. It seems morphologically logical to extend the concept of the botanical module to include the products of any single shoot apical meristem. The modular components of some sympodial axes are indeterminate and continue to grow as short shoots long after having been evicted to a subsidiary role (Hallé, this symposium). The inception of a new branch in a plant is practically always due to the activation of a single apical meristem. It is the control of such an act that forms the foundation of development in any branching system (see, for example, Thornley 1977).

## 2. BRANCHING

A single line is rarely the shortest distance between three (or more) points; branching and efficiency go hand in hand in the control of space. This universal phenomenon presents a universal problem: how to describe, analyse, and understand the rationale of branching systems, particularly if the system is dynamic and apparently becoming progressively more and more complex. Oxnard (1980) emphasized the need for a diversity of method in the analysis of form and advocates recourse to the new problem-solving techniques in subjects far removed

from biology. Branching systems occur in many guises throughout the biological and physical worlds. They are studied by mathematicians (graph theory; see, for example, Biggs *et al.* 1976) and by crystallographers (Mackay 1975). Geographers use the mathematicians' graph theory to devise transport systems (Haggett 1976) as do agronomists interested in root systems (Fitter 1985). Geomorphologists studying river basins have abandoned branch ordering systems as a means of quantification (Jarvis 1977) in favour of the mathematicians' trees (Smart 1978) and neuroanatomists have done likewise (Van Pelt & Verwer 1984). Botanists, lagging behind as usual, apply bifurcation ratios to real trees (see, for example, Oohata & Shidei 1971; Barker *et al.* 1973; but see Tomlinson 1978). The zoologist finds on a crinoid the same branching transport system for harvesting a resource and conveying it to a mouth (Cowen 1981) as a road research laboratory proposes for a banana plantation (Tanner 1967). The very precise branching tunnel system of an extinct ctenostomate bryozoan (Pohowsky 1978) in the shell of a mollusc is uncannily like the branching pattern of many plants or indeed similar to the pattern of veining in their leaves. It is likely that whenever the construction of the form of branching patterns is to be deciphered, the combination of the concept of modularity and computer-aided analysis will be invoked, for example in the analysis of the axon arborizations of a cat's spinal cord (Réthelyi 1981) or the biological control of a clonal weed (Room 1986).

Describing a branching organism in modular terms may not be too difficult, but recognizing interactions of these components, particularly in a developing sequence, presents many problems. It is crucial, however, to find a profitable compromise between simplicity, which has many attributes, and the complexity that will invariably result from attempts to incorporate some hypotheses related to the internal interactions between components.

### 3. COMPUTER SIMULATION

Any object or process can be modelled or imitated and the intentions for so doing vary enormously. Easy access to computer facilities has created a frenzy of simulations in every field of science (Wolfram 1984). Nearly 1500 computer models in environmental biology alone are listed by Kickert (1984), often unwittingly with similar goals and identical names. There is already a taxonomic crisis looming in the modelling world.

'A model represents the isolation of certain features of a complex situation so that their mutual relationships can be seen without the distraction of other features of lesser significance' (Mackay 1975). With this in mind, some simulation models of branching structures have been designed specifically and purely as teaching aids. Typical examples involve the growth and architecture of forests and their management. For example 'CROGRO' (Fellows *et al.* 1983) simulates the growth of crowns of trees as they compete for space and light. Decades of growth are condensed into a few minutes to demonstrate this process. The ability to speed up events is one of the useful byproducts of a growth simulation. 'TIMECOGS' (Welty *et al.* 1985) provides the student with a stand of timber trees portrayed graphically in a manner allowing the observer to walk among them. Individual trees grow better if their neighbours are removed. The student can practice the art of thinning without damaging a forest, and follow the outcome to harvest. An exceedingly convincing and aesthetic three-dimensional simulation of tree shapes is described by Aono & Kunii (1984, figure 21). The applications of this system as envisaged by the authors include graphic design, photogravure production for magazines and landscape gardening. These authors are aware of the modular nature of their trees and use empirical data in some

cases. Superb three-dimensional graphic simulations of real tree form based on contemporary interpretations of tree architecture (Hallé & Oldeman 1970; Hallé *et al.* 1978) are currently being produced by Jaeger and co-workers (1985).

The zoological application of computer simulation to form has frequently had a different objective. The assumption is made that change in the simulation 'rules' may mimic an evolutionary change in the genome of the organism. Raup (1966) showed that just four parameters were needed to simulate the gross form of the coiled shell and that actual specimens are not randomly distributed in the total spectrum of theoretically possible forms generated by computer. A more specific simulation, concerned with coiling in ammonoids (Raup 1967) again concluded that during the evolutionary development of ammonoid form only a small part of the geometric range available was represented. This leads to a consideration of the geometric problems of particular theoretical shapes and the conclusion that successful spirals represent compromises that satisfy a number of functional constraints. The computer alone can generate the 'missing' and supposedly unsuccessful shapes: 'In studying the functional significance of the coiled shell, it is important to be able to analyse the types that do not occur in nature as well as those represented by actual species' (Raup & Michelson 1965). Creating a simple simulation programme that can orchestrate a complex structure thus gives some possible indication of the level of complexity of controlling mechanisms. Raup (1968), referring to echinoid growth, stated 'the actual biological system controlling plate patterns need not be more complicated than that used in the computer simulation'. Similar statements appear in Ede & Law (1969) for vertebrate limb morphogenesis, Raup & Seilacher (1969) for foraging patterns of sediment feeders, as a general concept in Cohen (1967) and Gould (1970), and at the cellular level in fossil plants (Niklas 1977).

A simulation of the range of branching morphologies found in fossil colonies of spiral bryozoans (figure 3) again was found to be feasible by using few growth rules (McKinney & Raup 1982). Manipulation of these rules, in a series of replicated simulation runs, highlights the important factors in determining this spiral architecture and shows that quite slight changes of rules produce distinctly different forms (such as the conversion of the form of an extinct spiral bryozoan *Archimedes* into the form of an extant cheilostome bryozoan, *Reliflustra cornea*). One conclusion reached by these authors is that such simulations of branching patterns may indicate forms yet to be realised.

The ability to create ranges of morphological form, surpassing that to be found in extinct or extant organisms, naturally leads to discussion of the course of phylogenetic changes (as for the simulated branching morphologies of early land plants in which the random element of pattern generation is debated (Niklas 1982; Waller 1984; Niklas 1984)). Indeed, an experiment of evolution has been conducted by Papentin (1973) and Papentin & Roder (1975) based on a model of the feeding patterns of sediment worms. A population of 'worms', starting with various 'rules' or 'genes' to control their meandering, compete for food. Some patterns prove to be more successful than others at this activity and these individuals are subsequently granted a greater probability of reproduction involving mutation and recombination of rules. These experiments highlight the pertinent aspects of successful space exploitation by one specific type of pattern (unbranched and meandering). Similar theoretical experiments with more elaborate branched patterns, but lacking the 'gene flow', are described by Bell (1984, 1985).

On occasion, the very process of constructing a computer simulation to reproduce a particular branching structure can be a useful experience in its own right, even without proceeding to

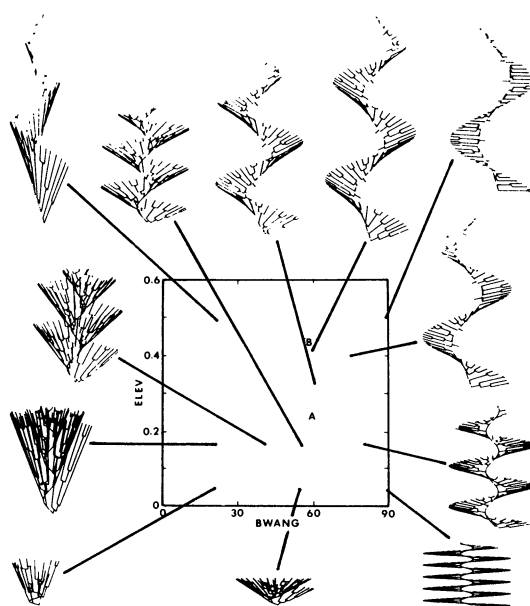


FIGURE 3. Simulated continuum of variation in the architecture of erect spiral bryozoans using few 'growth rules' (from McKinney & Raup (1982)). The extinct *Archimedes* is shown at top right and the extant *Reliflustra* centre bottom (see text).

the use of such a simulation to test an hypothesis. Either the morphology of the organism must be recorded in considerable detail or the underlying features of its developmental architecture fully appreciated, before an attempt can be made to model its growth. Shortcomings in the model will soon become apparent as 'mistakes', which are readily identifiable qualitatively but are not always easy to quantify. A subtle distinction has to be made in interpreting the output of a stochastic simulation between unintentioned teratologies, and the model's version of 'phenotypic' variation between replicates. Van Groenendael (1985) has shown how a model of developmental construction for *Plantago*, based on the modular concept, can be extended and used to construct and predict a wide range of teratological malformations that have been found in plantains. Such comparison of normal and mutant development aided by graphic modelling has likewise proved useful in the study of pea leaf morphogenesis (Young 1983).

In other instances it is the attempt to quantify phenotypic variation in branching pattern produced 'normally' by the organism that motivates the production of a branching model. Nishida (1980) set out deliberately to create tree-like structures based on *Chamaecyparis obtusa* (Japanese cypress) that have a built-in morphological variability similar to that found in nature between trees of the same clone; his intention was to use this controlled situation to quantify the degree of variability. In this manner, the majority of simulation models of branching are developed to test preconceived hypotheses. In this respect a model is not likely to be successful, or valid, unless it is predicted upon sound biological understanding of the growth processes that produce the morphology in question or upon an appreciation of the functional meaning of the morphology (Raup 1970).



## 4. THE CONTROL OF BRANCHING IN SIMULATION MODELS

A mathematician describes branching patterns in terms of a *junction* (or 'node') where a branch is inserted, and a *link*, the branchless connection between any pair of junctions. A graphical simulation of a branching process must control link length and thus junction location, branching angle, and most importantly branch potential: once the site for a new branch is fixed, will it grow? When will it grow? How will it grow? How will it die? Implicitly, such a simulation will be a process description of branching events and the majority of branching growth models are indeed dynamic. (An exception is the state description model comparing potential productivity in clones of *Populus* with different morphologies (Burk *et al.* 1983).)

Thus a branch simulation model 'grows' according to predetermined 'rules'. A rule controlling branch angle, for example, may be guessed at or based on empirical data and may incorporate a given variability. These aspects of rules of growth have been discussed recently by Lück & Lück (1982) and by Waller & Steingraber (1985). Waller & Steingraber classify growth rules as 'deterministic or stochastic', and 'stationary or non-stationary'. A deterministic branch model operates according to recursive rules that are precise and repeatable during the growth of the pattern and lack built-in random effects. Figure 4 illustrates momentary stages in the astogeny of three type of graptolites (using the simulation procedure of Bell *et al.* (1979)). Rules of growth are deterministic and also stationary, as they do not change (figure 4*a*) or change according to fixed rules (figure 4*b, c*). In these simulations a module is represented by a theca and each new branch is initiated by the production of an extra theca. The model of colony development in encrusting bryozoans produced by Gardiner & Taylor (1982) (figure 5) is likewise deterministic but is, however, non-stationary, branching being modified by interaction between modules, in this case represented by the zooids. The consequences of change in branching angle was investigated in terms of number of zooids per colony and resultant effective feeding area.

The nature of the rules used in the compilation of a branching model, stochastic, non-stationary and so forth, obviously depends on the instigator of the system. The nature of the 'rules' for branching and of their control in the actual modular organism is commonly ignored or unknown. In discussing the validity of such simulation models it is therefore important to identify this key factor: what events occurring within the artificially created organism supplement the control of branching imposed at the overall programme level? Three categories of branching simulation can be identified.

(i) 'Blind' patterns, in which branch initiation is controlled solely by the imposed programme rules, that is from without the 'organism' and its 'environment'.

(ii) 'Sighted' patterns, in which the initiation of a new branch is influenced by factors detected by it in the immediate neighbourhood, such as proximity of other organisms, or parts of the same organism.

(iii) Self-regulatory patterns, in which branch initiation is controlled by the developing simulation itself, using communication via components of the existing framework, whether or not affected by 'environmental' factors.

(i) '*Blind*' patterns

An example of a 'blind' pattern is the graptolite simulation referred to earlier (figure 4) and the complexity of such a pattern depends solely on the complexity of the imposed rules and

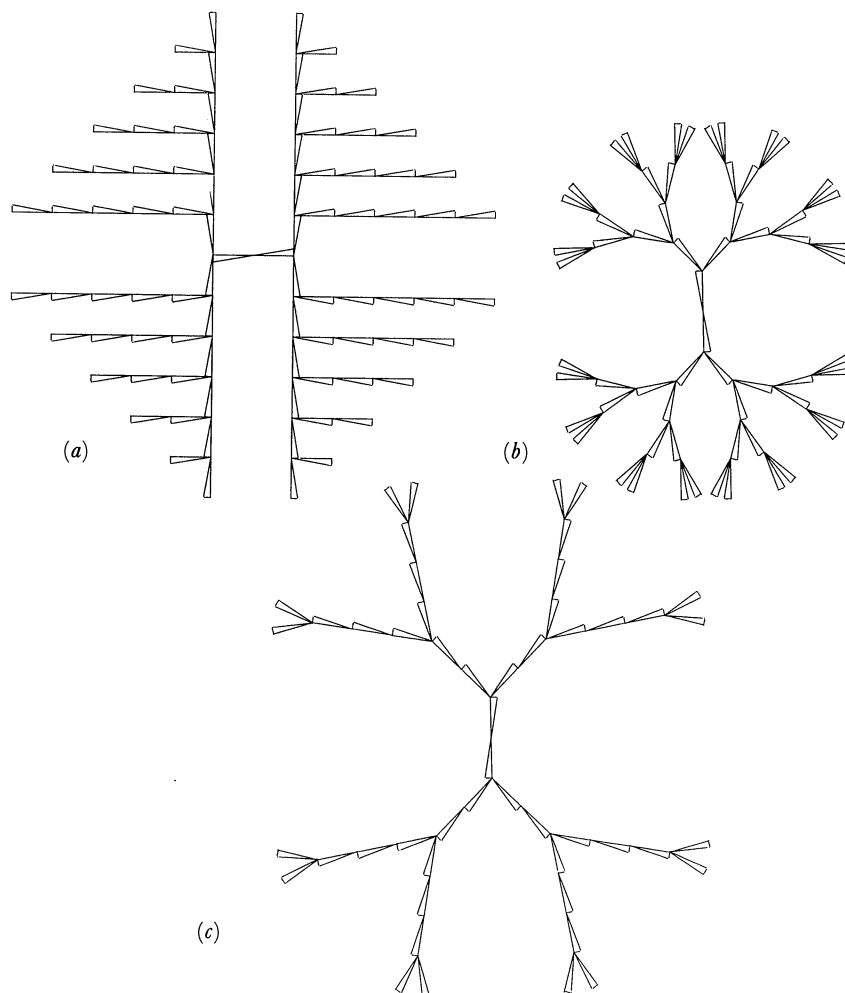


FIGURE 4. Deterministic, stationary simulations illustrating growth form in graptolites. An example of a 'blind' simulation. (a) Graptolite form with stationary rules for branch location and angle. (b) Graptolite form with stationary rules for branch location; branch angle rules also stationary but altering according to fixed rules (decreasing bifurcation in this instance). (c) Graptolite form with stationary rules; both branch location and bifurcation angle changing according to fixed rules.

the duration of the simulation. Hogeweg & Hesper (1973), using the Lindenmayer system for pattern description, were able to generate patterns of considerable complexity exhibiting unexpectedly realistic morphological features such as clustering of modules in short shoot complexes at intervals.

'Blind' patterns with simpler rules produced by Honda (1971), specifically to investigate problems in pattern morphogenesis and recognition, are described as 'tree-like bodies' and demonstrate the considerable variation in form that can result from small changes in branch angles and length ratios. Addition of empirical data to the Honda 'tree' simulations allowed Fisher & Honda (1977) and Honda & Fisher (1979) to study the efficiency of leaf display in the tropical tree *Terminalia* by comparing simulations of actual branch and leaf layouts with theoretical alternatives (see figure 8a-d). A similar simulation study has been conducted by Cheetham *et al.* (1981, 1983) into the efficiency of branching (and thus of feeding by rows of zooids) in adeoniform bryozoans (figure 6).

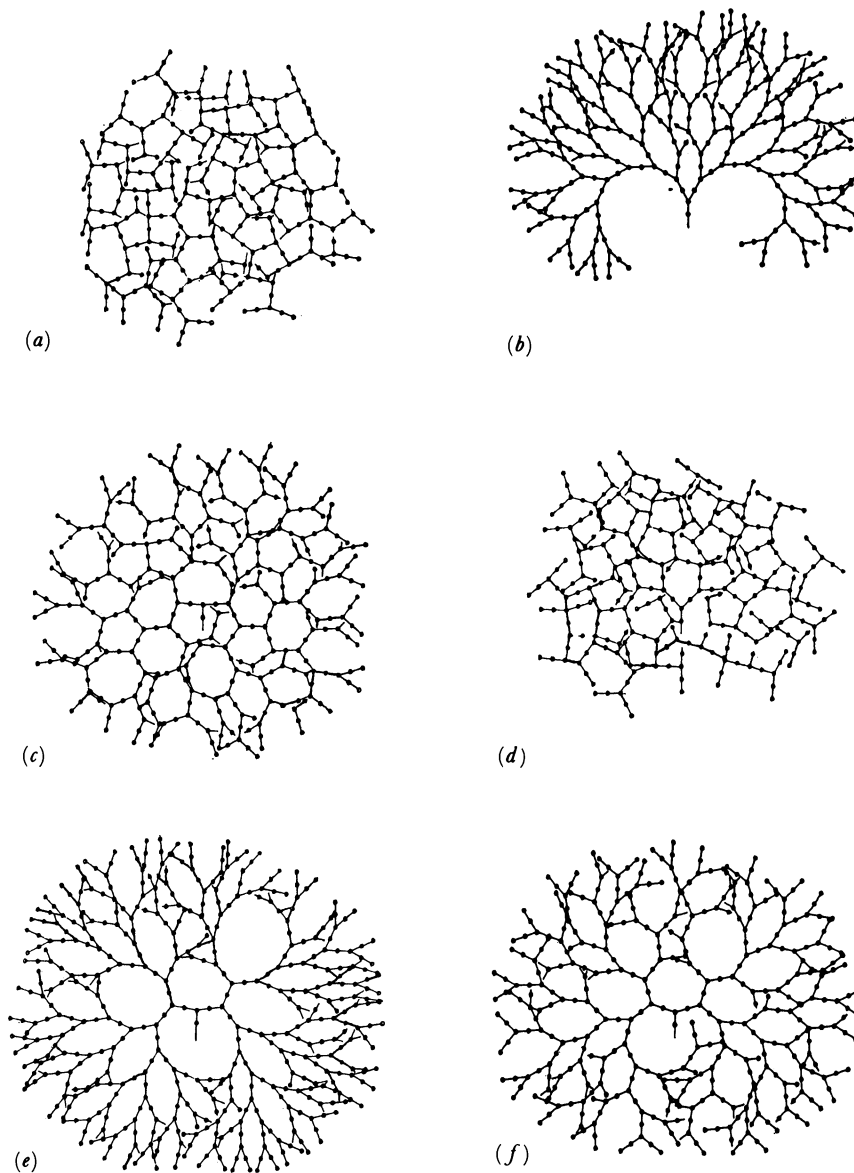


FIGURE 5. Artificial colonies of the fossil encrusting bryozoan (*Stomatopora*, a cyclosome) showing the change in form resulting from change in angle. These are 'sighted' patterns as branch growth is disrupted by proximity of neighbours. (From Gardiner & Taylor (1981)). (a) Constant large bifurcation angle; (b) constant small bifurcation angle; (c) constant decrease in angle; (d) constant increase in angle; (e) arithmetically decreasing angle; (f) exponentially decreasing angle.

(ii) '*Sighted*' patterns

'Sighted' simulations in which branching is influenced by external factors are demonstrated by Gardiner & Taylor (1982) (bryozoans, figure 5) and Cowen (1967). Honda *et al.* (1981) also introduced a branch interaction into their tree branching model by means of 'a horizontal circle of inhibition' located at the current terminal point of any branch, invasion of which influenced subsequent bifurcation (figure 8 *l-o*). A similar detection of available space governs the growth and bifurcation in the lateral branches of the simulation of spiral bryozoan

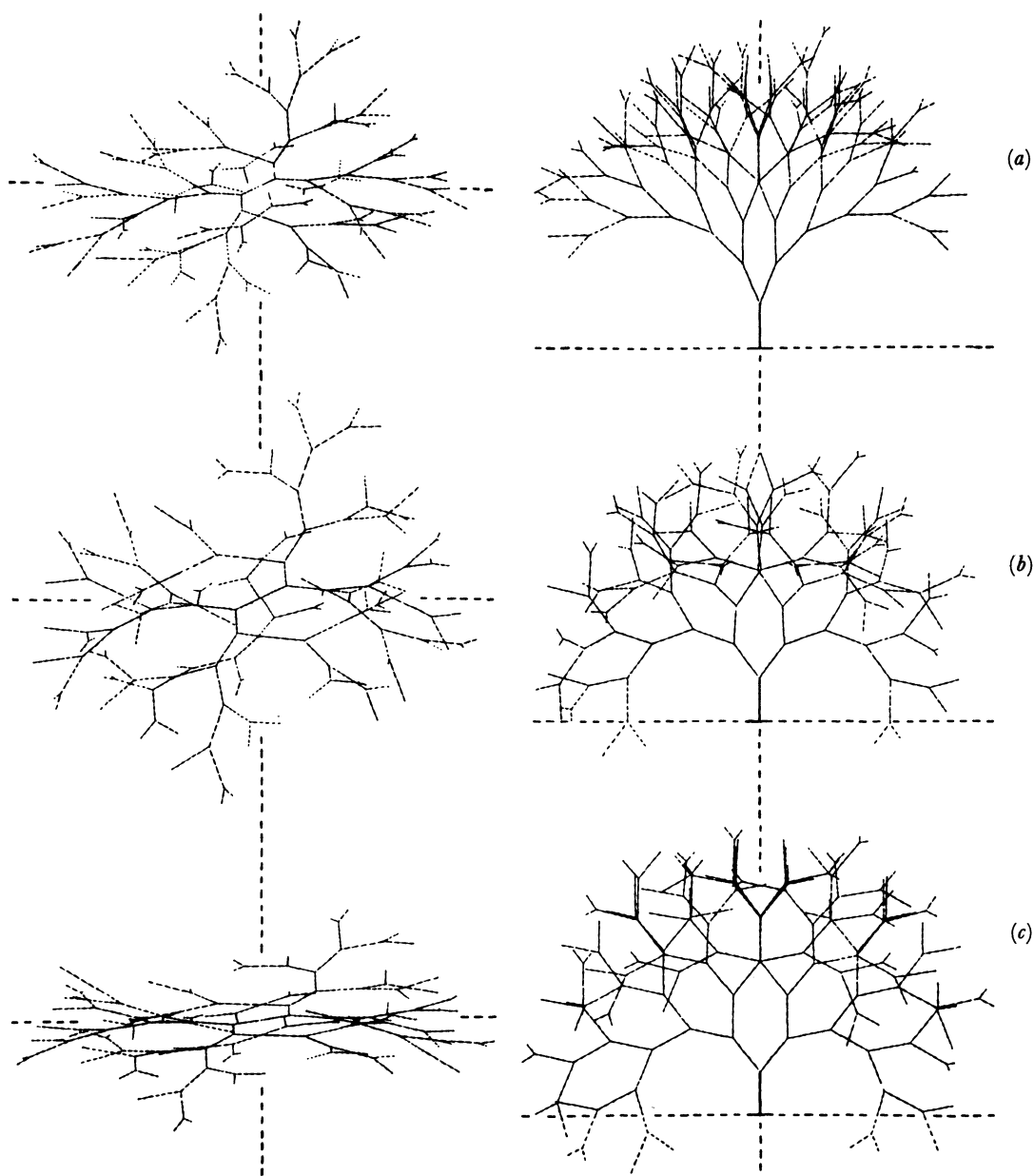


FIGURE 6. Simulation of form in arborescent bryozoans produced to study effectiveness of different geometries in terms of branch interference and zooid feeding efficiency (from Cheetham & Hayek (1983)). Top views on left, corresponding side views on right. (a), (b) and (c) The forms produced by three possible combinations of growth rules governing bifurcation angle and angle of twist between one bifurcation and the next. Combination of angles maximizing colony height do not coincide with those maximizing colony width or radial symmetry. Branching angles also affect the proportion of segments lost by reaching the substrate (shown as dotted lines in (b) and (c)). Angles: (a) bifurcation  $50^\circ$ , twist  $50^\circ$ ; (b) bifurcation  $80^\circ$ , twist  $50^\circ$ ; (c) bifurcation  $80^\circ$ , twist  $20^\circ$ .

architecture by McKinney & Raup (1982) (see figure 3). Such simulation of interference within developing patterns can demonstrate phenomena that would not otherwise be immediately apparent. Figure 7 (Bell 1985) illustrates that a threshold exists at a branch angle of  $23^\circ$  for this particular sighted pattern, above which a monopodial astogeny is possible, but below which a sympodial system is substituted due to abortion of apices in response to overcrowding.

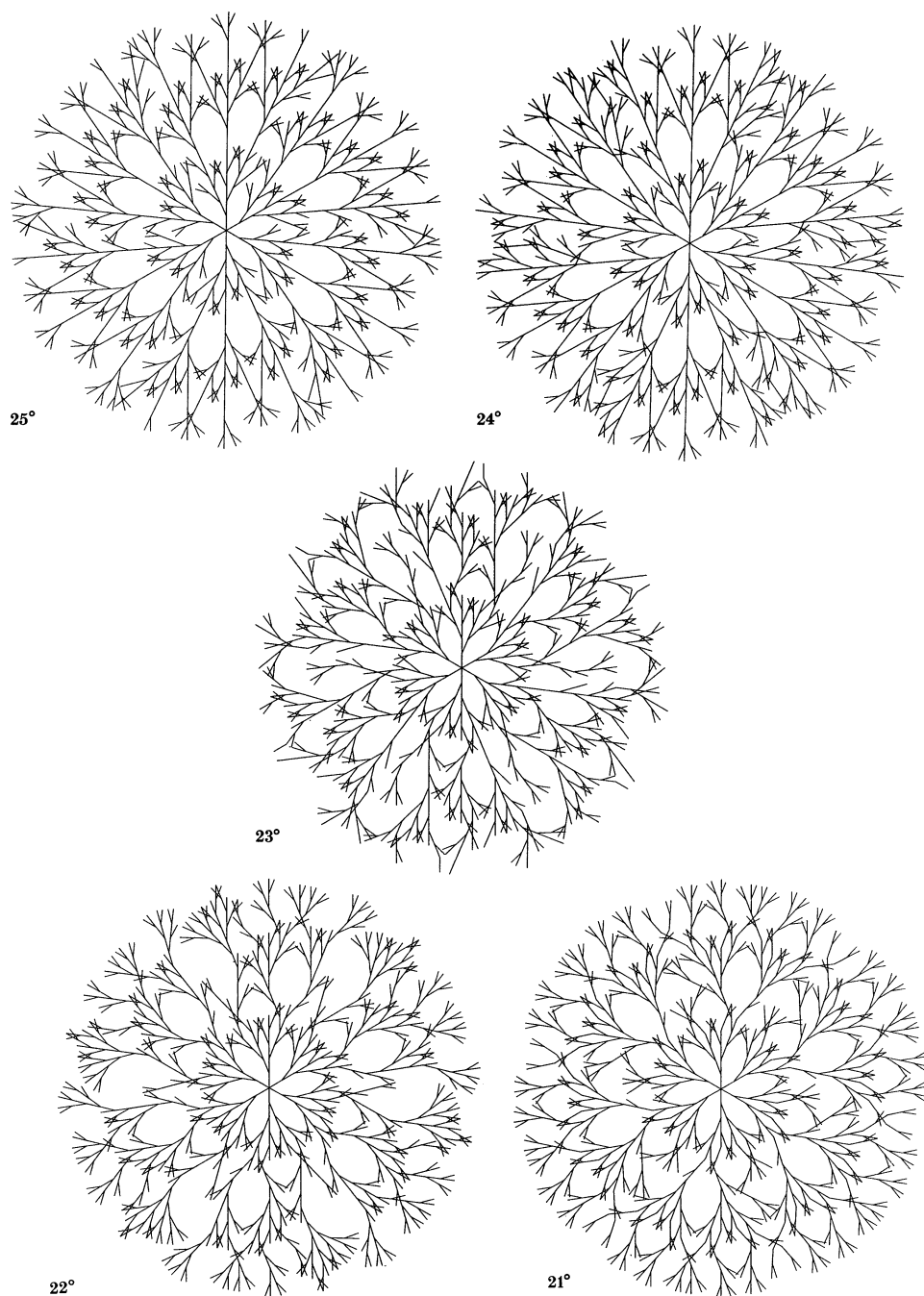


FIGURE 7. Five hypothetical patterns developing radially. Deterministic growth rules are identical in all respects except for lateral branch angles. Rules specify monopodial growth but this is superseded at narrow angles by abortion of crowded apices resulting in the production of sympodial growth. The fundamental switch from monopodial to sympodial branching results at a  $1^\circ$  change of branching angle ( $24^\circ$  to  $23^\circ$ ). (From Bell (1985).)

The underlying blind 'growth rules' for this simulation call for monopodial growth, but a sympodial development, due to the sighted component, actually materializes.

Sighted simulations incorporating response to interference monitored by a search routine assume that some detection process operates in the real organism, such as a response to shade or touch or release of a chemical. Very little is as yet known about such systems.

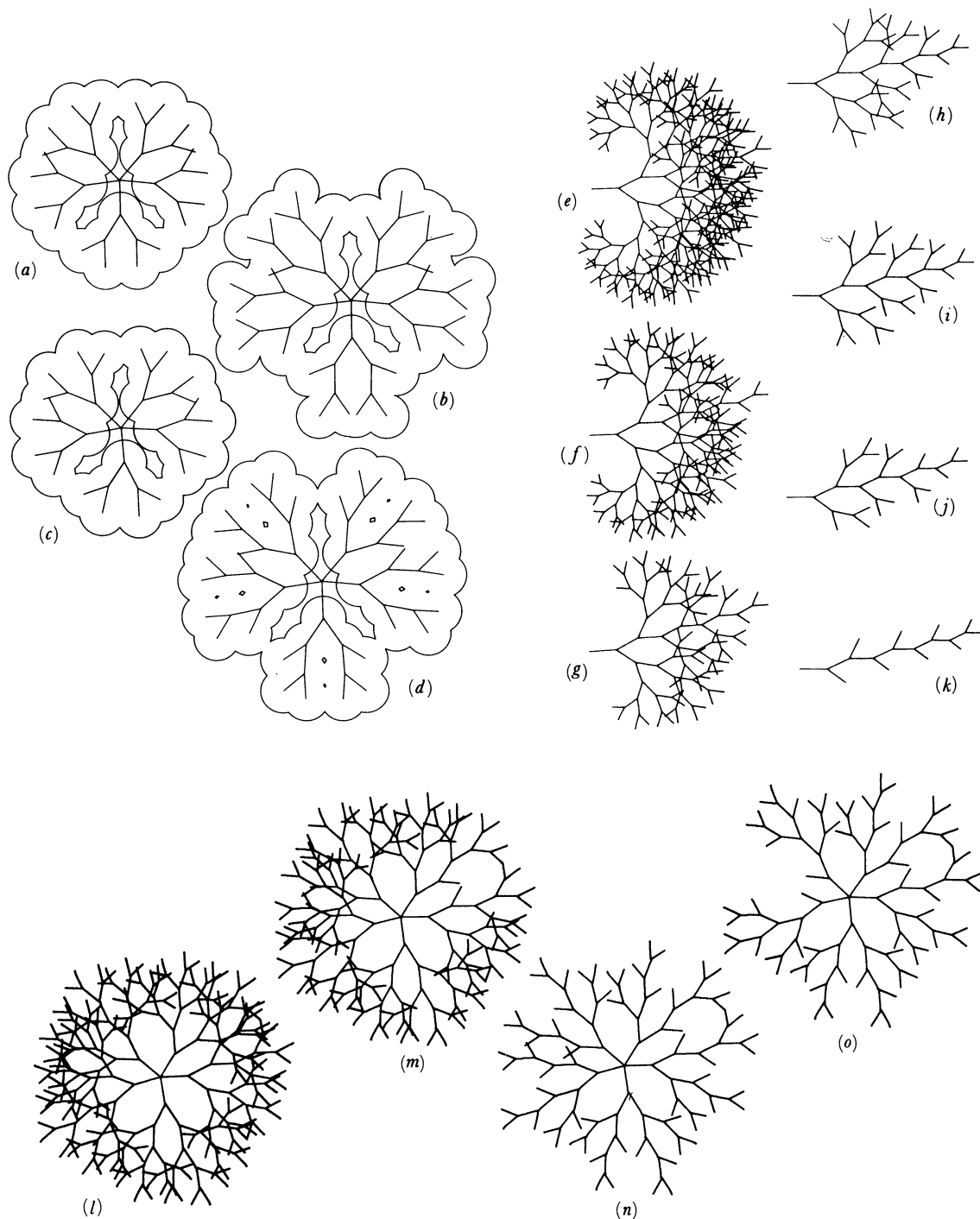


FIGURE 8. Simulation of horizontal tiers of branching in a tropical tree, plan view (*Terminalia*).

(a)–(d) ‘Blind’ patterns. Change in effective leaf display (represented by a circle centred at each bifurcation point), resulting from change in angle and asymmetry of bifurcation.

(e)–(k) ‘Self-regulatory’ patterns. Branching controlled by flow rate of a bifurcation factor within the developing pattern. (e) Equal flow to each side of a bifurcation (ratio 1:1). (k) No flow to one side (ratio 1:0). Ratios for (f)–(j) set at 1:0.998, 0.9, 0.66, 0.5 and 0.33, respectively.

(l)–(o) ‘Sighted’ patterns with progressively greater radius of search from distal ends for neighbouring branches that will prevent continued growth.

(a)–(d) From Fisher & Honda (1979); (e)–(o) from Honda *et al.* (1981).

(iii) *Self-regulatory patterns*

In self-regulatory patterns new branches, although they may be located by deterministic rules, are only initiated in response to events or conditions occurring within the developing simulation. One of the earliest branch simulations, that of Braverman & Schrandt (1965), operated in this manner. Continued stolon growth, hydranth location and type in a branching model of a marine hydroid (*Podocoryne*) was controlled by internal positioning factors based on assumed potential biological mechanisms.

Self-regulatory, internal control is also built into the inflorescence simulations of Frijters (1976, 1978*a, b*) (using versions of the Lindenmayer branch simulation system; Frijters & Lindenmayer 1974). Frijters recorded that a purely deterministic description of the developmental architecture in *Aster* would become too complex because each branch would require its own separate instructions. Instead, growth of side branches is controlled by information obtained about its neighbours. Similarly in a model for *Hieracium*, branch initiation and flowering sequence are controlled from within the developing simulation by 'flow of auxin'.

The series of studies of tree branch architecture by Honda & Fisher (1979) referred to above have recently been enhanced by recourse to self-regulatory simulation models. Unequal branch lengths at bifurcation points in *Terminalia* can be controlled by unequal flow rates of a 'bifurcation factor' (figure 8) (Honda *et al.* 1981). Some simulated patterns controlled by this means proved to be similar to those observed in actual trees. The simulated geometry and development of branching in another tree, *Tabebuia rosea*, was organized again from within the system by 'flux distribution' (Borchert & Tomlinson 1984; Borchert & Honda 1984). In these simulations self-regulatory mechanisms control branching vigour, potential and asymmetry while feedback systems within the development framework confer the equivalence of apical control.

A final example of a self-regulatory system is illustrated in figure 9 and represents the first stages of a simulation model under development based on the system of Bell *et al.* (1979). Figure 9*a* shows a developing clover (*Trifolium repens*) stolon at plastochron nine. The apical meristem of the main axis and the apical meristems of buds in the axil of leaves only grow if they receive, via the framework of the simulation, sufficient 'photosynthate' from exporting leaves. Leaves only export photosynthate if they are not being shaded. Figure 9*b* is an identical simulation in all respects except that the leaves have four exporting leaflets rather than three. The clover in figure 9*b* will suffer reduction in photosynthate production because of its more congested canopy, and therefore shelf shading, but will enjoy greater photosynthate production because of its larger number of leaflets. The outcome, by plastochron nine, is the earlier activation of specific bud apices as close scrutiny will reveal. This outcome cannot be predicted.

The self-regulatory branch models developed so far are crude, and are based on insecure hypotheses of physiological mechanisms. Nevertheless, the combination of sound morphological branch description, whether computerized or not, and better knowledge of physiological controls must assist the understanding and manipulation of modular growth.

## 5. CONCLUSION

In different branched modular organisms there is varied correspondence between the identity of the module and the nature of the links in the branch framework. For example, the 'module' in a bryozoan is represented by a zooid but branch initiation in such an organism may begin

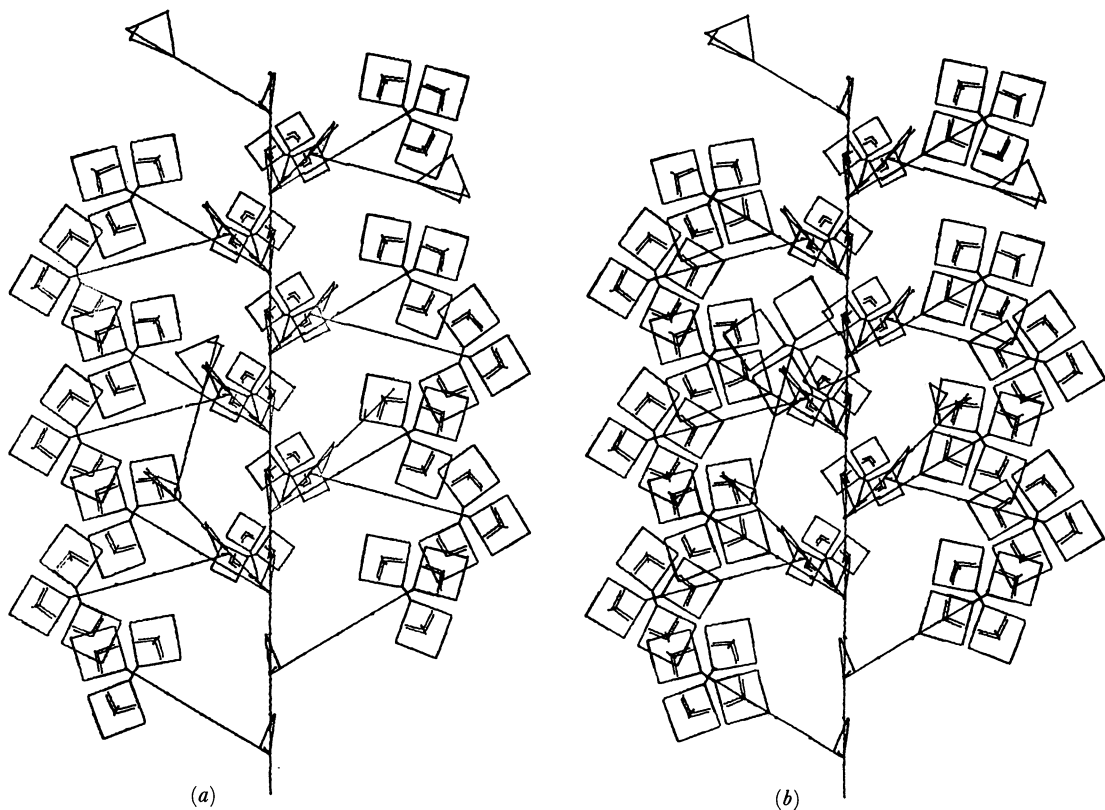


FIGURE 9. A self-regulatory and 'sighted' simulation of white clover stolon growth. Growth of buds is controlled by photosynthate exported from leaflets. Leaflets fail to produce photosynthate if they detect overtopping (shading) by other leaflets. (a) Three leaflets per leaf, (b) four leaflets per leaf, identical simulations otherwise. On balance, greater self-shading in (b) is over-compensated by greater export, and the four-leaflet clover is developing faster.

with the development of a single extra zooid (encrusting cyclostomes), or a group of zooids (arborescent cheilostomes). In higher plants branch initiation is represented by the development of a new apical meristem, and thus new module. Nevertheless, whatever the relationship of module to branch, the lynchpin in branching astogeny is the control of new branch initiation.

Branching architectures are readily simulated by computer graphics. Again, in the manipulation of such developmental forms, it is the control of new branch initiation during the simulation that can distinguish different levels of biological reality. These are described here as 'blind' (simulated organism oblivious of its environment), 'sighted' (each branch initiation influenced by its surroundings but unaware of its connectivity within the organism), and 'self-regulatory' in which astogeny is controlled from within the developing organism using internal and possibly external information. The growth of real modular organisms may be controlled by various combinations of these three factors and simulation may provide an insight into their functioning.

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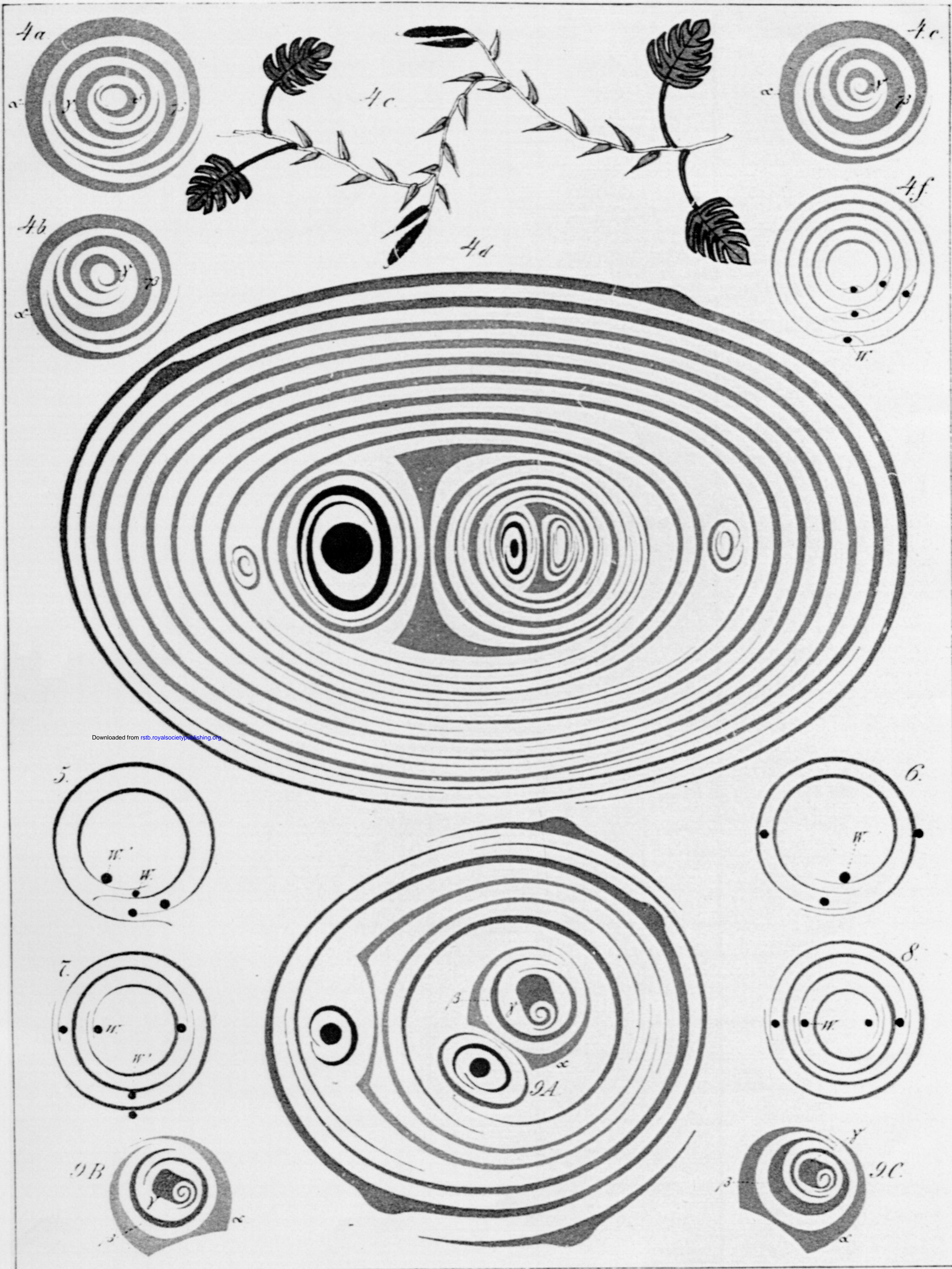


FIGURE 1. A 'floral' diagram. A traditional state description of plant form (from Engler (1876)).