# EFFECTS OF SIMULATED GROWTH PARAMETERS ON BRYOZOAN COLONY FORM

By

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# ABSTRACT

## EFFECTS OF SIMULATED GROWTH PARAMETERS ON BRYOZOAN COLONY FORM

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This study provides a framework for the simultaneous computer simulation and analysis of mechanisms which, synergistically, can produce the external forms of bryozoan and other animal colonies.

Erect, non-flexible, double-walled stenolaemate bryozoans are the main focus, by virtue of the integrated, individual-like nature of their colonies, which produce a wide variety of forms by varying relatively few mechanisms.

Computer programs keep track of the state of an astogenetic system as the timing, or rates, of some mechanisms are altered, while the rest remain unchanged, allowing a suite of astogenies, analogous to developmental differences between related forms, to be simulated. Variability can be simulated easily at individual, micro-evolutionary, and even at high taxonomic levels.

It is determined that in order to maintain extensive growth of branching bryozoan colonies, bifurcation inhibition and growth-direction modifying mechanisms must be employed. The importance of incremental growth and founder effects in astogeny is stressed.

Listing of independent astogenetic parameters and

suggestions for their use in ontogenetic and evolutionary studies are given.

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# INTRODUCTION

<u>Bryozoans and computer simulation</u>- The purpose of this study is to analyze, via computer simulation, the development of some common types of bryozoan colonies in order to understand better the possible mechanisms contributing to their external shape.

The use of computer simulations of biological form in both individual development (ontogeny) and the development of colonies (astogeny) is hardly original. It dates nearly to the time computers first became available to biologists and geologists and workers in allied fields. Harbaugh and Bonham-Carter (1970) provide a good review of these, in addition to a wealth of fascinating techniques and related ideas. Raup (1972) reviewed and classified all the kinds of simulations attempted in paleontology as of that time. Niklas (1977) reviewed numerous computer reconstructions of fossil plant ontogenies with comments on the theory of simulation. Many computer simulations of fossil animals are also available, including the deterministic coiled shell studies initiated by Raup and Michelson (1965), which has been modified recently (McGhee 1978) to allow for a more realistic simulation of accretionary growth. Stochastic (random) parameters were first introduced into simulation programs independently by Raup and Seilacher (1969) in a fossil foraging behavior (trace fossil) simulation and by Waddington and Cowe (1969, p. 189) in a study of snail shell pigmentation patterns. Raup (1969) predicted that further development of stochastic models was to be expected in more biologically plausible situations,". . . as, for example, the morphology of colonial corals. . . ." However, computer assisted analyses of the development of animal colonies are sadly lacking. Although viable and even mathematically tractable models of bryozoan colony growth are available (Kaufman 1970, 1971, 1973, 1976; Wass 1977; Thorpe 1979; Blake 1979; McKinney 1979, 1980), only one attempt to actually simulate a bryozoan's colony form with the computer has been so far published, although only in abstract form (Gardiner and Taylor 1980). Their study attempts to analyze the astogeny of a small vine-like bryozoan, Stomatopora, and succeeds in producing some realistic results by introducing a random variable (presumably normally distributed) with standard deviations provided by empirical data. There apparently are no computer simulations of other colonial animals. Therefore, it would appear that there exists no specific framework for the computer simulation of the mechanisms producing the external form of animal colonies. This study provides one. Bryozoans are the chosen subject of this study because in no other group of organisms of comparable taxonomic stature has more diversity in form been based upon a common ground plan. From their simulation an approach is developed that is potentially applicable to all colonial animals.

Bryozoans: the analysis, the Bauplan- The basic phylogenetic rules for the biology of the Bryozoa (Ectoprocta), or the bryozoan Bauplan, can be briefly stated as small (individuals are virtually microscopic), coelomate (very possibly eucoelomate), most likely deuterostomes, colonial (a few individuals to millions), and lophophorates (all lophophorates, including brachiopods and phoronids have a food gathering apparatus adjacent to their mouths bearing ciliated tentacles for generating feeding currents). The classification scheme provided by Cuffey (1973) will be followed in the ensuing text when referring to the higher taxonomic levels. The conventions illustrated by Gautier (1970) will be used when referring to various views in thin-sections.

Although some bryozoans have only a gelatinous sheath covering them, most build hard chitinous or calcareous skeletons which can be preserved as fossils. The mode of construction of these skeletons bears on the development of colony form and differs somewhat from group to group among bryozoans. Since the majority of extinct bryozoans found in ancient (especially Paleozoic) shelf sediments are stenolaemates (Tubulobryozoa), special emphasis is placed on their construction. There are two basic modes of colony construction in stenolaemate byrozoans: the double-walled and the single-walled habits (Figure 1a,b). There is also a relatively rare form (Brood 1976) which mixes these two modes in somewhat comparable proportion (Figure 1c). It is important to note that a double-walled colony has a single-walled portion to its base and a single-walled colony has double-walled construction in its marginal growing zones. An important feature of the double-walled growth mode is that there is a colony-wide fluid-filled space, called the hypostegal coelom, that can function as a medium for the transport of nutrients, hormones, and other dissolved substances (Schopf 1977). Some single-walled bryozoans have developed communication pores through the walls separating individual zooids to bring about the functional equivalent of the hypostegal coelom. The characteristic intracolonial transport of nutrients and hormones allows certain parts of the colony to be free to specialize as functional polymorphs and is considered (Boardman and Cheetham 1973) to increase greatly the degree of colony dominance. This factor is the major consideration in the decision of whether to treat certain animal colonies as groups of individual organisms (populations) or as single entities. It is important to distinguish between the ontogeny of individuals, as such, within colonies and that of colonies as a whole when one is

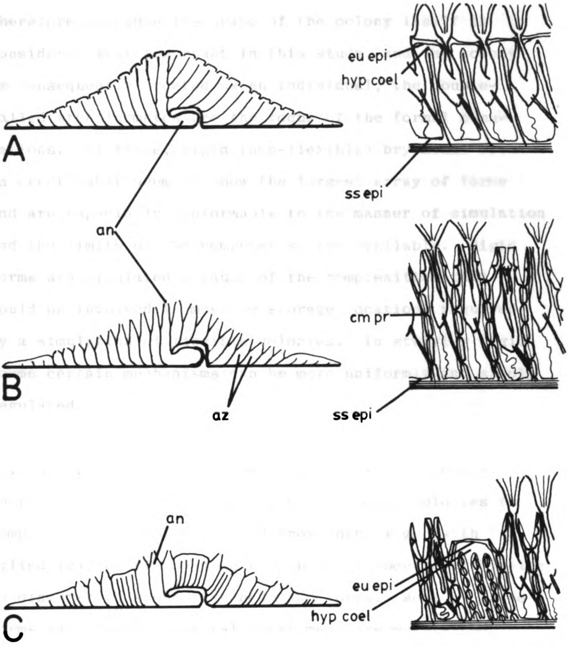


Figure 1. Different modes of bryozoan colony construction. a, double-walled; b, single-walled; c, mixed type. eu epi = eustegal epithelium, hyp coel = hypostegal coelom, ss epi = skeleton-secreting eqithelium, cm pr = communication pore, an = ancestrula, az = autozooid.

considering the evolution of aspects of colony form. Therefore, because the shape of the colony itself is considered most important in this study, and the colony is consequently treated as an individual, the double-walled stenolaemates are the focus of the formal simulations. Of these, rigid (non-flexible) bryozoans with an erect habit seem to show the largest array of forms and are especially conformable to the manner of simulation and the limits of the computer system available. Rigid forms are simulated because of the complexities that would be involved in movable storage locations required by a simulation of flexible colonies. In studying rigid forms certain mechanisms can be more uniformly and simply regulated.

Colony forms in double-walled byrozoans range from unilaminar encrusting sheets to glob-like and hemispherical colonies, from tall slender ramose colonies to complete net-like fronds, and from thin twigs (with cylindrical or ribbon-like branches) of about a millimeter in diameter to stout-branched stony forms. Most of these forms range across several taxa; many are maintained within the range of a single species' norm of reaction. Many of the differences between the forms listed can be shown to be merely quantitative and produced by variations in the action of identical mechanisms (see Tavener-Smith, 1974 for discussion of this idea in the Trepostomina, Rhabdomesita, and Ptilodictyita; and Tavener-Smith 1975, for the discussion of homologies between the Fenestrina and Ptilodictyita). Such mechanisms, because of similar problems arising from common life habits analogous forms in the single-walled and other bryozoan taxa and may be applicable to non-bryozoans of similar growth habits.

For the purposes of the simulation, the generalized double-walled stenolaemate will be considered a colony that starts with a single founder individual (called an ancestrula) which initiates the growth of the colony by forming a recumbent common bud (Borg 1926) out of some of its epithelial and mesodermal tissues which spreads distally (outward in a radial fashion from the ancestrula, see Figure 14a-f). It usually grows first in one direction and then "back-budding" occurs and it then grows in the opposite direction, eventually forming a disc. The common bud is also free to spread vertically, but usually doesn't until later on in astogeny. (See, however, McKinney 1978, for some important distinctions exhibited by the Fenestrina.)

The hypostegal coelom is present even in the advancing edge and the entire colony is covered by a chitinous cuticle. The epithelium under the hypostegal coelom, or zooidal epithelium, secretes a calcereous basal wall between itself and the cuticle underneath, which is resting on the substrate. The edge continues to expand this way while more proximal (closer to the ancestrula) secondary skeleton is being deposited over the basal wall as nearly recumbent dividing walls. These split up the common bud into tubular areas (called zooecia) that will house the individual zooids. The zooecial walls grow, first in a recumbent manner, subparallel to the growth of the basal wall, but later turning until they are nearly at right angles to the surface of the colony. As they grow thusly, they bring parts of the zooidal epithelium into close proximity with the epithelium above the hypostegal coelom (or eustegal epithelium), but the two epithelia do not merge and the coelom remains continuous. This is the fundamental difference between double-walled and single-walled bryozoan colony, where the hypostegal coelom is still continuous, new zooecia can still form but not where the base and "roof" have fused to form a single wall. As the zooecia grow, their apertures become more and more widely spaced (Figure 1b). In a double-walled bryozoan, however, the common bud still potentially exists anywhere on the surface of the colony but is usually localized as individual budding centers some distance from the advancing edge of the colony base. As the zooecia grow distally, the spaces that develop between them may be filled by newly-budded zooecia. In small erect forms, this budding center begins to bud zooids in a vertical direction and eventually forms an erect stem which may then continue to grow vertically, budding zooids, and later may bifurcate to form new axes of growth and budding.

In larger forms, several budding centers seem to develop and to display a spacing mechanism between one another. (Anstey et al. 1976). From this, the importance of budding pattern and zooecial shape to the external form of a bryozoan colony should be apparent. However, the effect of zooid shape is probably less in double-walled stenolaemates than in single-walled ones due to the countersunk nature of their apertures.

One more characteristic of the double-walled bryozoans should be considered for the purpose of the simulation. The zooecial walls are not usually of uniform thickness throughout their length. As the zooecial walls begin to turn from their original recumbent position, they begin to thicken, in some species smoothly and slightly, but in others curtly and with great differences in thickness between this outer, exozone and the inner, recumbent endozone. The differences in wall thickness in endozone and exozone seem correlated, if not dependent on the different growth rate associated with the two areas. Figure 2 shows the differences in location of endozone in exozone in a typical trepostome skeleton showing the relative positions of the two. The endozone is always associated with the fast-growing axial regions of branches and stems. Diaphragms, transverse partitions in zooecial

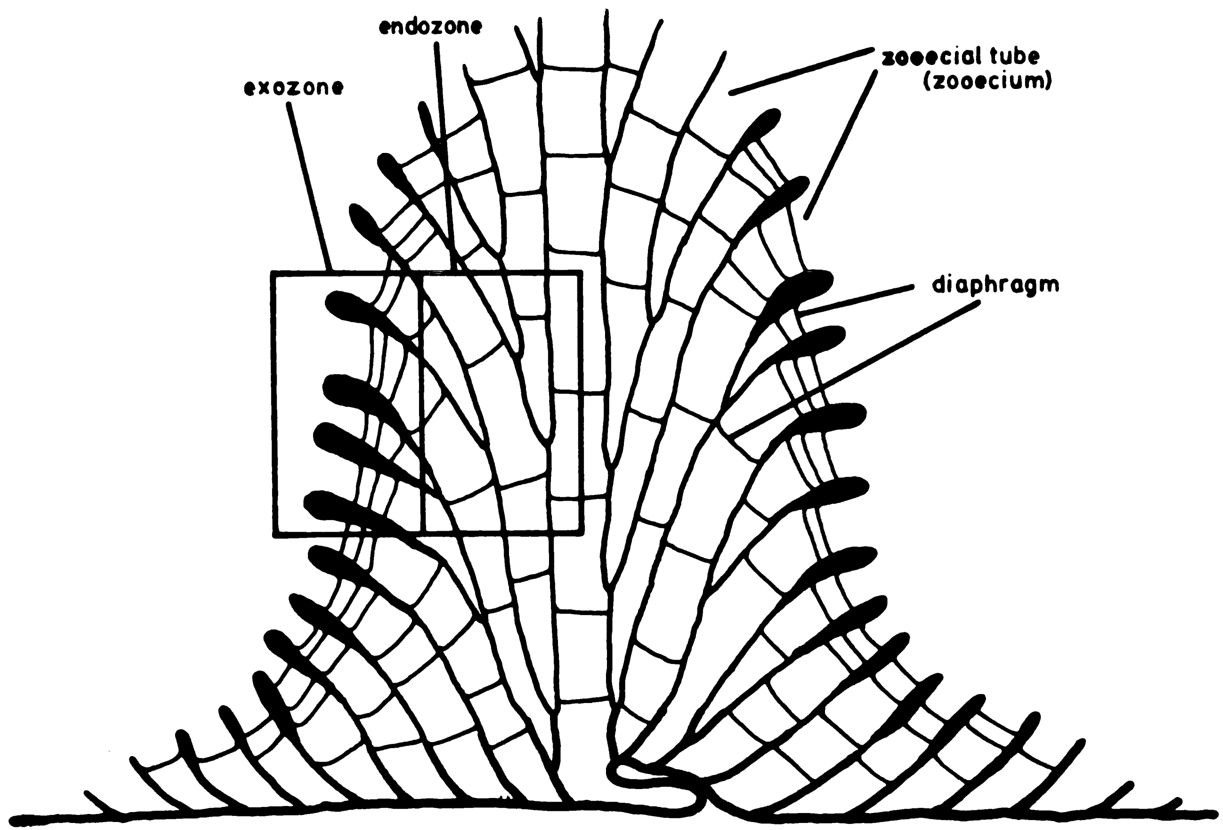


Figure 2. The locations of exozone and endozone in a typical trepostome.

tubes which may be laid down at regular intervals, are widely spaced here (when they occur). The exozone is associated with the periphery of a branch, where growth is slow, budding slow and localized, and diaphragms are normally closely spaced in taxa where they occur. Thus, the endozone's contribution to colony shape is to lengthen and determine the original width of a branch, while the exozone gives additional thickness to the colony as a whole (see Figure 2).

The potential for macroevolutionary study and heterochrony- The documentation of evolution in the fossil record is traditionally one of the noblest pursuits in paleontology. Some early bryozoan workers, considering colonies as individual organisms sought to show recapitulation in lineages by demonstrating how zooids forms characteristic of the late astogeny of ancestral forms are found earlier in the astogeny of descendants (Lang 1904; Cumings 1910). They called this process tachygenesis (although nowadays it is usually referred to as acceleration). It is a way of producing evolutionary change by altering the timing of the developmental processes which, along with a few similar processes, comes under the general heading of heterochrony.

A computer can keep track of the state of a developing system as the timing for one or more mechanisms is altered while the rest remain unchanged. This would allow a suite of ontogenies (or astogenies) to be simulated that would be analogous to the developmental differences between different points in evolving lineages as they appear in the fossil record. Thus, if the astogeny of a single species of bryozoan can be satisfactorily simulated, and the proper freedom of reaction is built into the program, a change in a single parameter may produce a satisfactory simulation of an ancestor or a descendant. Changing the value of another parameter may produce a form which is never known to have existed. Raup (1969) stated that the simulation of real species and intermediate but unknown forms may help to understand better the relationships between the known forms and the evolutionary processes that separate them. By simulating these forms at the level of the developmental mechanisms a simulation is one step more realistic than one at the level of the organism and, by virtue of that distinction, the analysis of that simulation is one step more valid for the study of evolutionary change than the analysis of one that seeks to simulate form directly.

Changes in developmental timing that take place among populations and produce new species are best considered under the heading of macroevolution. Those that take place within a population and work to produce genetic variation, which can serve to better adapt a population by providing the substance of natural selection, are best considered under microevolution. Those that take place within a single colony occur within a single genotype (in bryozoans anyway) and, therefore, must be considered under ecophenotypy or norm of reaction, as the differences between individuals with exactly the same genes must be considered environmentally, or perhaps also, astogenetically produced. The computer simulation, as it knows no distinction between ancestral and descendant species, between regional races, or between one member of a population or another, can simulate each of these three levels with equal facility, as long as they involve changes in timing. The potential is great for future research. If evolutionary changes and ecophenotypic changes can be simulated with equal facility and, if simulations producing a wide range of known and unknown forms can give insights into evolutionary processes, then perhaps simulations of ecophenotypically real and unknown intermediate forms may give insights to environmental processes.

<u>The nature of the algorithm</u>- According to the classifications of Harbaugh and Bonham-Carter (1970), this simulation would be a "dynamic hybrid." That is, it is dynamic because it has "state" variables that hold the values of some specific characteristics of the system modelled, such as "current dry weight" or "amount of surface area this iteration," that can change during the course of the simulation and potentially give feedback to

the system. It is a hybrid because it contains both deterministic and stochastic components. That is, in the case of deterministic variables or parameters, they are either given as constants or else are precisely predictable at any point in the simulation from the beginning. In the case of stochastic variables or parameters, they are not precisely predictable and the best we can do is predict the limits within which they will fall by a certain time in the simulation. There are actually two programs which were used in various simulations and a modification of the first which allows the simulation of forms where zooid shape is very important in determining the shape of the colony. This modification (BBK) was not implemented in the analyses related herein but is included in Appendix I so that it will be available for future reference. The first program (DWBBF) considers many of the features of an erect branching and encrusting double-walled bryozoan of limited size. The next program (AASP) is especially designed to deal with problems incurred by planar or reptant (vine-like) colonies with extensive distal growth and numerous bifurcations with various special mechanisms to deal with their consequent complexity. The former is capable of higher resolution than the latter. The programs were written in FORTRAN Extended, Version 4 and were designed to run on Michigan State University's Scope/Hustler system featuring a Cyber 750 digital computer with a Calcomp plotting facility. Program development was done interactively. Programs were either submitted to the input queue after having their parameters modified interactively or, if short, run interactively. Output was in the form of plots. DWBBF had its plots as perspective drawings rotated about various axes and AASP plotted a two-dimensional plan view of the colonies simulated. The two programs were designed to supplement each other, one simulating more details in the smaller sized colonies where resolution is important and the other simulating patterns in the extensive colonies where pattern is more important.

There really is very little in this simulation that is truly original, but it does combine several of the best ideas from other simulations. Raup and Michelson (1965) simulated the coiled shell, which in nature grows by incremental accretion. They used a continuous function, changing three parameters to produce a wide variety of forms. But the model was static and deterministic and, although the form generated very closely approximated the shape of real shells, the simulation was of the shape and not truly the ontogeny. In addition, the approach used could not be applied to organisms with non-gnomonic growth (i.e., where juvenile stages do not appear, as in gnomonic growth, to be proportioned the same as, but smaller than, the adult stage). McGhee (1978) altered the model by adding state variables to maintain the position of the growing edge of the shell and introduced growth vectors and incremental growth, thus making the model a true simulation of ontogeny, and the potential applicability of the model was taken out of the realm of gnomonic growth (although that study chose to remain there).

Gardiner and Taylor (1980) built in two stochastic components to their Stomatopora model and provided the flexibility to use them in their growth vectors. In this way a certain degree of realism was achieved. The simulation used in the present study makes use of incremental growth and state variables, growth vectors and stochastic components, and the flexibility of growth vectors is extended to the third dimension. The approach to simulation taken also maintains the same generality as in the original coiled shell simulations, but is applicable to non-gnomonic growth.

With the proper amount of built-in freedom, a simulation will not only have realistic results but possibly serendipitous and potentially heuristic results. In a good physical simulation (for example, an airplane in a wind tunnel), if one tests a model under certain constraints, one can predict, with a fair amount of confidence, what will occur in nature. This is possible in a good symbolic simulation too, as presented herein.

## THE SIMULATIONS AND RESULTS

Attempts, limits, regrets- A computer simulation of double-walled erect bryozoans was designed based upon the approach outlined in the introduction. The programs (see Appendix I) were designed to start with a small founder zooid (or group of zooids closely associated with the founder), go through a series of growth iterations, and while doing so, simulate various aspects of the astogeny of a bryozoan colony, in order to produce a form that crudely, but not superficially, approximated the external form of a real colony (see Figure 3). The major limitations to this simulation are size and resolution, which can be traded for one another. If greater resolution was required, a smaller area had to be simulated. The program capable of higher resolution (DWBBF) has a memory manipulation feature which allows a two-dimensional array of sixty-bit integer words to hold a three-dimensional image. This is done by considering each of the sixty binary bits in each word as a point in the third dimension. Individual bits were accessed, for storing the position of a filled space or to determine whether a space was already filled, with the use of the MASK and SHIFT operations available in the FORTRAN Extended intrinsic function library available at Michigan State's computer laboratory. After the simulation of astogeny is finished, the image, stored in the colony storage array, is accessed, one bit at a time,

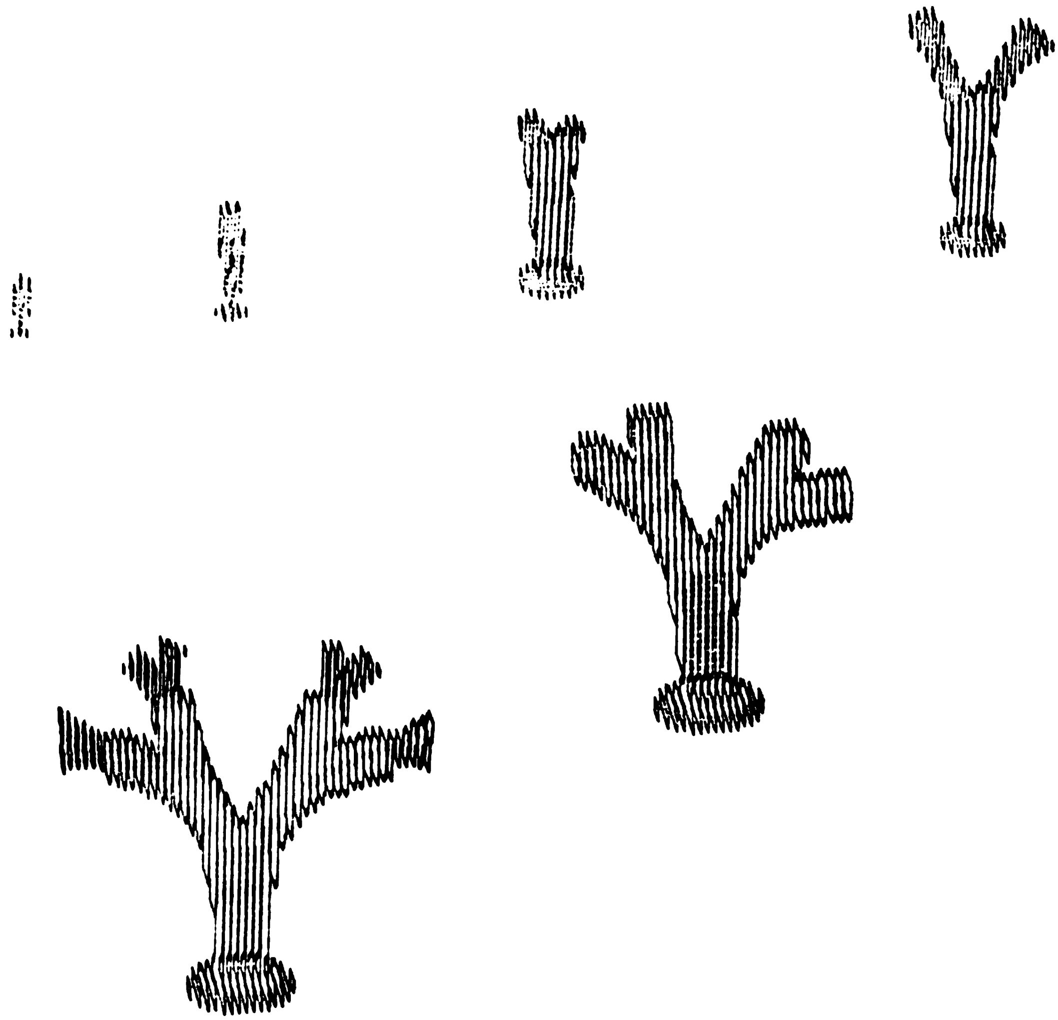

Figure 3. A simulation of an astogenetic series.

and used by the plotter to make its perspective drawings. The extensive colony program (AASP) has a somewhat simpler design and represents branches as line segments, which are plotted as they are generated. The positions of branch segments are stored in their own unique variables as each can be considered a colony in itself. This latter program differs from the former in that the positions of colony parts are stored in variables naming the parts instead of the parts being stored in variables that name the positions. However, both seem equally effective in the simulation of rigid forms, while the simulation of flexible ones would be greatly facilitated if the colony parts remained part of the system and only their positions changed.

The simulations done for this thesis included a series for use in the analysis of branch shape and development, particularly the first axis arising from the colony base, and the first few bifurcations. Another study was made of the complexities brought on by extensive bifurcation and distal growth in two dimensions. An algorithm for extensive growth in three dimensions has yet to be developed.

<u>The framework of the simulation</u>- A brief walk-through of programs, of loops and subroutines, will facilitate the individual descriptions to follow. Listings of the actual code are given in Appendix I. The two programs are essentially similar and only the manner of data storage and retrieval and the order of data transferal to the plotter

are different. Besides these, the extensive growth, low resolution program, AASP, is a much simplified version of the high resolution program, DWBBF. For the purpose of the walk-through the high resolution program will be followed. Figure 4 is a flow chart describing the basic functions of the program and the major decisions made during a simulation. A list of state variables and parameters important to the simulation is given in Table 1. Rankings of parameters in terms of importance, for DWBBF and AASP are given in Tables 2 and 3, respectively.

First the parameters are read. They consist of various constraints, limits, rates, and other information necessary for the desired simulation (see Table 1). Then a large loop begins to execute through the number of iterations requested. Then a second, smaller loop, completely contained in the larger, begins executing, the number of times depending upon the number of branch axes there are at its start. In the standard simulation there is one, initially. This one is vertical and represents the first part of the generalized double-walled colony to raise itself above the substrate. Later, more axes may be added, up to a specified limit, and the inner loop will execute one time per iteration for each of them. However, as this loop makes up a major portion of the larger loop, which in turn comprises most of the largest subroutine in the program, the addition of many branches greatly increases the

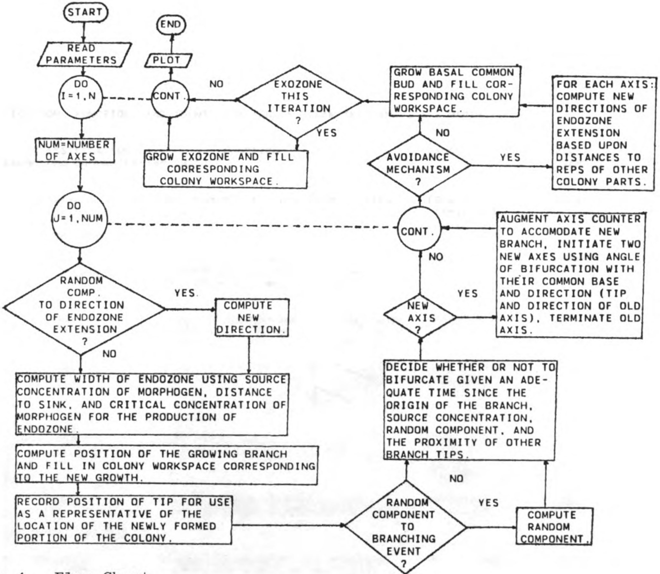


Figure 4. Flow Chart.

TABLE 1. CLASSIFICATION, FUNCTION, AND IDENTIFICATION OF PARAMETERS AND STATE VARIABLES



| VARIABLE | CLASSIFICATION (Harbaugh and Bonham-Carter 1970) | FUNCTION | RANGE | VARIABLE NAME(S) | TYPE |
|---|---|---|---|---|---|
| Number of iterations | Static Deterministic | Sets number of iterations in simulation. | (Greater than 0.) | ITERAT | INTEGER |
| ENDOZONE WIDTH PARAMETERS: | | | | | |
| Critical concentration of endozone promoting morphogen | Static Deterministic | Sets minimum concentration of morphogen required in a location to produce endozonal growth. | (Greater than 0.) | CRITCO | REAL |
| Maximum concentration of morphogen at source. | Static Deterministic | Sets the maximum level of morphogen production at the point source. Also used to limit bifurcation,q.v. | (Greater than 0.) | CMAX | REAL |
| Initial growth rate of the morphogen concentration | Static Deterministic | Assuming the initial source concentration is zero, this parameter sets the rate of increase, per iteration of the morphogen at its source. | (0. to CMAX, Greater than 0.) | DSCINI | REAL |
| Degree of elliptical eccentricity conferred by the mesotheca | Static Deterministic | Sets the elliptic radii for endozone transverse outline. | (Usually set to 1.) | H | REAL |
| | | | (0. to 1., greater than 0.) | KAY | REAL |
| Distance from source to sink | Static Deterministic | Sets the distance between the the morphogen source and its sink. | (Greater than 0) | ISNK | INTEGER |
| ENDOZONE WIDTH STATE VARIABLES: | | | | | |
| Width of the endozone | Dynamic Deterministic | Stores the value of the endozone width for a particular branch axis. | (0. to ISNK) | RWIDTH(N) | REAL |

TABLE 1 Continued



| VARIABLE | CLASSIFICATION | FUNCTION | RANGE | NAME(S) | TYPE |
|---|---|---|---|---|---|
| Endozone-morphogen source concentration | Dynamic Deterministic | Stores the value of the concentration of the morphogen at its source. | (0. to CMAX) | SCONC(N) | REAL |
| Growth rate of concentration of endozone morphogen at source | Dynamic Deterministic | Stores the value of the current per-iteration growth rate of the morphogen concentration at its source in a particular branch. | (0. to CMAX) | DSCONC(N) | REAL |
| ENDOZONE EXTENSION AND GROWTH DIRECTION PARAMETERS: | | | | | |
| Endozone extension rate | Static Deterministic | Sets the per-iteration rate of distal endozone extension, and thus the lenthening rate of the branches. | (Greater than or equal to 0.) | GR | REAL |
| The angle of bifurcation | Static Deterministic | Sets the angle at which the endozone morphogen point sources and, consequently, the branches bifurcate. | (0. to 180. degrees) | ANGLE | REAL |
| The amount of ran-random play in branch growth direction | Static Deterministic | Sets the limits of three standard deviations on a normally distributed random component to branch growth direction. | (0. to 180. degrees) | PLAY | REAL |
| Random component to branch growth direction | Static Stochastic | Generates a continuous normally distributed pseudo-random number for use in determining random errancy in the growth direction of a branch. | (0.-1.) | RANDND | REAL |
| Critical distance for inclusion in growth direction gradient of avoidance mechanism | Static Deterministic | Sets the maximum distance for a colony part from a growing tip for it to be considered on the tip's avoidance mechanism. | (Greater than or equal to 0.) | CRDIST | REAL |

TABLE 1 Continued



| VARIABLE | CLASSIFICATION | FUNCTION | RANGE | NAME(S) | TYPE |
|---|---|---|---|---|---|
| The magnitude of the avoidance reaction | Static Deterministic | Sets the amount of weight the avoidance gradient has with respect to the branch's own growth vector. | (Greater than or equal to 0.) | AVMAG | REAL |
| ENDOZONE EXTENSION AND GROWTH DIRECTION STATE VARIABLES: | | | | | |
| Components of the growth vector | Dynamic Hybrid | Store the X-, Y-, and Z-components of the growth vector, whose norm is the endozone extension rate (GR), for a particular axis. | (-GR to GR)<br>"<br>" | AXIS(N,1)<br>AXIS(N,2)<br>AXIS(N,3) | REAL<br>"<br>" |
| Coordinates of individual representatives of various portions of the colony | Static Hybrid | Stores the X-, Y-, and Z-coordinates of individual representatives of colony parts for use in determining the avoidance gradient. ("Reps" are formed from the locations of each branch tip after every iteration.) | (unlimited, but usually 0. to 60.) | REP(N,1)<br>REP(N,2)<br>REP(N,3) | REAL<br>"<br>" |
| Number of representatives of various colony parts | Dynamic Hybrid | The number of reps is used in the construction of the avoidance gradient. | (0-1000) | NREPS | INTEGER |
| BIFURCATION TIMING PARAMETERS: | | | | | |
| Period of growth between bifurcations | Static Deterministic | Sets the average number of iterations between bifurcation events. | (Greater than 0) | ITBIFU | INTEGER |
| The amount of random play in bifurcation timing | Static Deterministic | Sets the limits of three standard deviations on the normally distributed random component to bifurcation timing. | (0.-ITBIFU) | RNDBIF | REAL |

TABLE 1 Continued 

| VARIABLE | CLASSIFICATION | FUNCTION | RANGE | NAME(S) | TYPE |
|---|---|---|---|---|---|
| Random component to bifurcation timing | Static Stochastic | Generates a discrete, normally distributed random component for use use in determining bifurcation timing. | (Unlimited, but normally between -RNDBIF and RNDBIF) | IRAND | INTEGER |
| Critical distance for bifurcation inhibition | Static Deterministic | Sets the maximum distance at which one branch tip may inhibit another from bifurcating even though the timing be proper. | (Greater than or equal to 0.) | BFDIST | REAL |
| Physiological limit for morphogen source bifurcation | Static Deterministic | Observations indicate that the first bifurcation of an erect stem often takes longer (assuming constant endozone extension rate) than subequent ones. Thus, the stem is simulated as not being able to bifurcate until the concentration of morphogen has reached CMAX at its source. | (Greater than or equal to 0.) | CMAX | REAL |
| BIFURCATION TIMING STATE VARIABLES: | | | | | |
| Time since last bifurcation | Dynamic Hybrid | Stores the current age of an endozone morphogen source, and thus the age of a branch. Found by subtracting the number of the iteration in which the branch began from the current iteration number. | (Greater than or equal to 0) | NUM-ITIME(N) | INTEGER |
| Coordinates of individual branch tips | Dynamic Hybrid | Stores the coordinates of individual branch tips for use in computing distance to a branch tip being considered for bifurcation for comparison with the critical distance for branch inhibition. | (Unlimited, usually from 0. TO 60.) | TIP(N,1)<br>TIP(N,2)<br>TIP(N,3) | REAL<br>"<br>" |

TABLE 1 Continued

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| VARIABLE | CLASSIFICATION | FUNCTION | RANGE | NAME(S) | TYPE |
|---|---|---|---|---|---|
| Number of branch tips | Dynamic Hybrid | Stores the number of branch tips for the purpose of limiting a "DO LOOP" which compares distances to a certain tip for the consideration of bifurcation inhibition. | (0 to 32) | KAXIS | INTEGER |
| Endozone morphogen source concentration | Dynamic Deterministic | Stores the value of the concentration of the endozone morphogen at its source for a particular branch and is used to determine physiological ability to branch. | (0. to CMAX) | SCONC(N) | REAL |
| BASAL ENCRUSTING MECHANISM PARAMETERS: | | | | | |
| Linear rates of substrate encrustation | Static Deterministic | Sets the elliptic radii for the growth of the basal common bud as it spreads out over the substrate. Parameters are in terms of basal spreading rate per iteration in the X- and Y-directions. | (Usually set to 1.)<br>(0. to 1.) | XCOMP<br>YCOMP | REAL<br>" |
| BASAL ENCRUSTING MECHANISM STATE VARIABLES: | | | | | |
| Coodinates of the current edge of the colony base | Dynamic Deterministic | Stores the position of the current edge of the colony base which is a site for further accretion; only empty, adjacent spaces are eligible. | (Unlimited, but usually 0 to 50) | COLONY(X,Y) (see below) | INTEGER |
| Current iteration number | Dynamic Deterministic | Stores the value of the current iteration, this is multiplied by the linear rates of substrate encrustation to find the elliptical radii of the colony base. | (1 to ITERAT) | NUM | INTEGER |

TABLE 1 Continued



| VARIABLE | CLASSIFICATION | FUNCTION | RANGE | NAME(S) | TYPE |
|---|---|---|---|---|---|
| EXOZONAL GROWTH PARAMETER: | | | | | |
| Rate of exozone thickening | Static Deterministic | Sets the rate at which the exozone thickens, expressed as the number of iterations required to increase the exozone thickness by one unit position in the memory workspace. | (Greater than 0, if the period is greater than ITERAT, no exozone grows.) | XEXO | INTEGER |
| EXOZONAL GROWTH STATE VARIABLE: | | | | | |
| Position of available colony surface eligible for exozone growth | Dynamic Hybrid | Stores the coordinates of all the currently filled (and empty) bits in the workspace. Bits which are empty and adjacent to filled positions would be eligible for exozonal growth. | (0 to 1) | COLONY(X,Y) (see below) | INTEGER |

Note: The array "COLONY(X,Y)" holds the memory storage image of the entire colony. Each word in the array represents a vertical column in an XY-grid. Each bit in the integer word represents the height of a point in space. Thus a bit with a value of one represents a filled space, and a bit with a value of zero represents an empty space which is a certain height above the base. When the array is used to find the basal common bud, only the bottom layer is used.

TABLE 2. A RANKING OF THE PARAMETERS IN DWBBF IN TERMS OF IMPORTANCE



| RANK | NAME(VARIABLE) | REASONS FOR IMPORTANCE |
| --- | --- | --- |
| 1. | Number of iterations(ITERAT) | Determines the ultimate size, extensiveness, and complexity of the simulated colony. |
| 2. | Endozone extension rate(GR) | Determines the existence and growth rate of all growth above the substrate. |
| 3. | Rate of exozone thickening(XEXO) | Determines the existence of all secondary growth on the colony surface and the rate of thickening of the branches. |
| 4. | Maximum concentration of endozone morphogen at the branch tips(CMAX) | Arbitrary threshold for the timing of the first dichotomy of the erect stem; also of prime importance in determining endozone width. |
| 5. | Critical distance for bifurcation inhibition(BFDIST) | Helps determine the density-dependent frequency of branching in extensive and complex colonies. |
| 6. | The magnitude of the avoidance reaction(AVMAG) | Determines the susceptibility of branch growth to re-direction in extensive colonies, greatly affecting final colony shape. |
| 7. | Critical distance for inclusion in the growth-direction gradient of avoidance mechanism(CRDIST) | Determines whether the avoidance mechanism, in a growing branch, will work only in response to nearby colony parts or to consider a larger portion of the colony; affects the apparent straightness of branches. |
| 8. | The amount of random play in branch growth direction(PLAY) | Removes perfect geometric symmetry from endozone growth and early dichotomies. This parameter is absolutely necessary in order to have a realistic simulation. |
| 9. | The angle of bifurcation(ANGLE) | Determines the initial angle at which branches may be expected to diverge, which greatly affects the shape of the simulated colony. It is made somewhat less important by random factors and growth-direction modifying mechanisms. |
| 10. | The amount of random play in bifurcation timing(RNDBIF) | Prevents perfect dichotomous branching by providing a range of random variation for branch timing. |

TABLE 2 Continued



| RANK | NAME(VARIABLE) | REASONS FOR IMPORTANCE |
|---|---|---|
| 11. | Period of growth between bifurcations(ITBIFU) | Determines the base rate for bifurcation timing, which will greatly affect the appearance of the colony. It is made somewhat less important by random factors and the bifurcation inhibition mechanism. |
| 12. | Distance from source to sink (ISNK) | Sets limits on the maximum width of endozone. |
| 13. | Critical concentration of endozone promoting morphogen (CRITCO) | Determines the endozone-morphogen level at which endozone begins to form and thus the timing between colony inception and the commencement of erect growth. |
| 14. | Initial growth rate of the of the morphogen concentration(DSCINI) | Helps determine growth rate of endozone width and timing for commencement of erect growth. |
| 15. | Degree of elliptical eccentricity conferred by the mesotheca(H;KAY) | Doesn't affect overall shape of colony, but causes flattening of of branches in colonies with low exozonal growth rates. |
| 16. | Linear rates of substrate encrustation(XCOMP;YCOMP) | Independent of erect growth; encrusting growth could be another entire study. Its simulation here is maintained primarily for perceptual convenience. |
| * | Stochastic parameters(RANDND; IRAND) | Greatly important in the simulation of ecophenotypic and other "unpredictable" effects, as well as adding a touch of realism, these parameters cannot be varied by the user and have no set value. Consequently their effect varies from one time to the next. As such, they are very important, but can't be ranked. |

TABLE 3. A RANKING OF THE PARAMETERS IN AASP IN TERMS OF IMPORTANCE

| RANK | NAME(VARIABLE) | REASONS FOR IMPORTANCE |
|---|---|---|
| 1. | Number of iterations(ITERS) | Determines the ultimate size, extensiveness, and complexity of the simulated colony. |
| 2. | Critical distance for bifurcation inhibition(BFDIST) | Greatly affects the pattern of zoarial growth in extensive colonies by governing the frequency of bifurcation. |
| 3. | The amount of random play in branch growth direction(PLAY) | Removes perfect geometric symmetry and is essential for realism in the study of pattern in extensive simulations. |
| 4. | Critical distance for inclusion in the growth-direction gradient of avoidance mechanism(CRDIST) | Determines whether the avoidance mechanism, in a growing branch, will work only in response to nearby colony parts or to consider a larger portion of the colony; affects the apparent straightness of branches. |
| 5. | Initial orientation of the five original axes(VAX/5. or VAX/18.) | Not available to the casual user, these alternative values represent two different sets of initial conditions for the simulation, and can be altered only by editing the program. Starting the program with the five initial branches constrained within 90. degrees of arc has been shown to lead to even spacing much sooner than when the five are spread evenly about a full circle. |
| 6. | The angle of bifurcation(ANGLE) | Usually set to 180. degrees, the ultimate (and most important for overall pattern) angle of branch divergence seems to be more strongly determined by the avoidance mechanism and the random factor to growth direction. |
| * | Stochastic parameter(RANDND) | Greatly important in the simulation of ecophenotypic and other "unpredictable" effects, as well as adding a touch of realism, this parameter cannot be varied by the user and has no set value. Consequently its effect varies from one time to the next. As such, it is very important, but can't be ranked. |

cost of a run, so that for the most extensively branched simulations the other program was used. (Indeed, this was a major reason for its creation.) Before any growth of the axis occurs, the random component (if one is required) to its growth direction is determined. Then a subroutine is called which determines the width of the endozonal area of the branch for the current iteration. Then the positions of points making up the newly grown portion of branch axis are determined according to the growth direction (which is the rate of lengthening of a branch during an iteration), and the endozone width. Refer to Table 1 for the functions of the parameters and state variables involved. The position of the new tip is then recorded for its possible use as the representation of the general position of the newly grown colony part in the event that another branch growing in the vicinity may seek to avoid anastomosing with it. After this, the decision of whether or not to bifurcate is made. This doesn't normally happen in every iteration of the outer loop and rarely during the first iteration. First, the random component to bifurcation timing (if one is allowed) is computed. Then, the decision is made based on the branch bifurcation timing parameters (see Table 1), the time since the branch was formed, the proximity of other branch tips (if the bifurcation inhibition mechanism is elected for the simulation), and the random component.

If the branch decides to bifurcate, the branch counter is increased by one, and two new axes are initiated; one given the state variable storage locations of the parent (which is thereby terminated) and the other given a fresh set. Then the inner loop finishes its iteration and, depending on its counter, decides whether to make another loop or go on into the outer loop again. When the outer loop is re-entered, the growth directions of the endozones of each branch may be modified so that they are less likely to grow into one another (that is, if the avoidance mechanism is elected for the simulation). Then the edge of the encrusting portion of the colony (the basal common bud) is grown according to its specified parameters (see Table 1) and the time since the start of its encrusting growth (normally the beginning of the run). Next, the exozone is grown. Because the exozonal walls grow much more slowly than the endozonal walls, the simulation doesn't normally grow endozone every iteration. If the exozone is to be augmented in the current iteration, the workspace is scanned for empty spaces adjacent to filled spaces and then fills them, so that the "colony" is covered with a new layer of exozone thickening previously covered areas and blanketing freshly grown branch axes heretofore consisting of only endozone. Then the iteration ends and loop decides to continue iterating or go on depending on the iteration counter. When the outer loop ends, the image in memory is stored in a permanent file for later reference, and then transferred to the plotter for output.

The growth of branches in space- If one considers for a moment the extension of endozone into the third dimension certain problems come to mind. Excluding physiological mechanisms accounting for the phenomenon and reducing the concept, for the moment, to one of a vector in space with a certain range of variation in direction (the random component), the problem becomes one of how the vector and its variability can be simulated. The original (and average, if there is a random component) vector itself, is easily represented in either Cartesian or spherical coordinates, but the actual vector used is more difficult to determine. If the amount of deviation from the true course of arrows on their way to a bullseye were expressed in terms of a normally distributed random variable with measurements taken from the center of the target, the standard deviation could be expressed as an angle (at least for fairly good archery). Thus, the amount of deviation about a vector can be simulated by a continuous, normally distributed, random variable. If the archer doesn't hit the bullseye, he can still hit above, below, and to the right or left. The scatter at a specific distance from the center should be fairly uniform (because they are all scored the same). Thus, the resting place of any specific arrow can be modelled by two random variables: one, normally distributed, which determines the amount of deviation from the true path; and a second, uniformly distributed one that determines which spot in the circle a certain distance from bullseye the arrow will hit. The second variable can be expressed as the angle that a line drawn from the arrow head to the center to the target makes with another, standard, line through the center (a vertical one, for instance).

Figure 5 shows how a specific growth vector (V') could be obtained from an initial vector with a certain amount of random variablity. The vector can be expressed in terms of four variables, in addition to its magnitude, and transformation from this system of "bipolar" spherical coordinates to Cartesian coordinates is included in Appendix II.

In essence, the initial growth vector is stored in terms of its X-, Y-, and Z-Components for convenience in evaluating the positions of branch tips and colony representatives for use in the avoidance and bifurcation inhibition simulation. Its components are translated into spherical coordinates, where PHI "$\phi$" is the angle measured, counter-clockwise, around the Z-axis from the XZ-plane. The vector's magnitude is stored. Then PHI PRIME "$\phi'$" is selected randomly from a normal distribution (see Appendix III, for continuous, normally distributed random number generator algorithm)

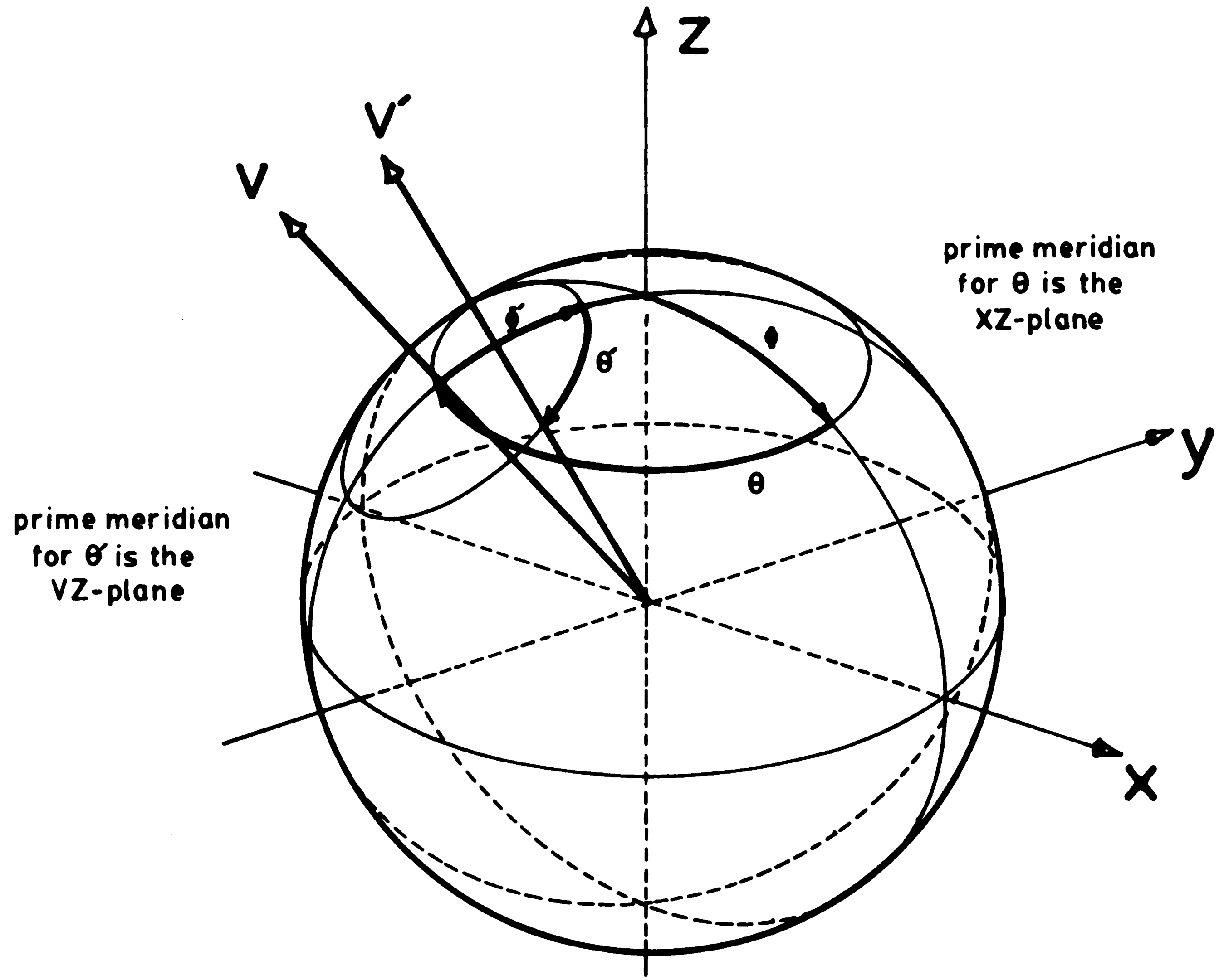


Figure 5. How a specific vector (v') could be obtained from an initial vector and random variability.

with mean zero and standard deviation set by a parameter that has been read in. Finally, THETA PRIME "$\theta$'" is selected at random from a uniform distribution (see Appendix III). Then the new vector is translated into Cartesian coordinates (see Appendix II) and replaces the old one in its storage location. Figure 6a shows the effect of varying the random component for branch growth direction in the simulation of a simple erect branching colony. This introduction of a random component to the growth direction has two main purposes in the simulation and may be widely applicable to other simulations of ontogeny where previously the random component had been confined to two dimensions. In the present situation, the random component, firstly, adds a touch of realism, also noted by others (Waddington and Cowe 1969; Raup and Seilacher 1969; and Gardiner and Taylor 1980), because it serves to simulate all the minor effects that cannot be identified individually as modifiers of form. This concept fully extends to and is intrinsic in all other stochastic simulations of any system. Secondly, it provides a founder effect. Because of a deviation in the early growth direction of a branch, the tip may be at a certain place at a specific time to influence the growth direction of bifurcation time of another branch (see Figure 14d, f for example). This is important because it appears to be a very close analog of many natural phenomena,

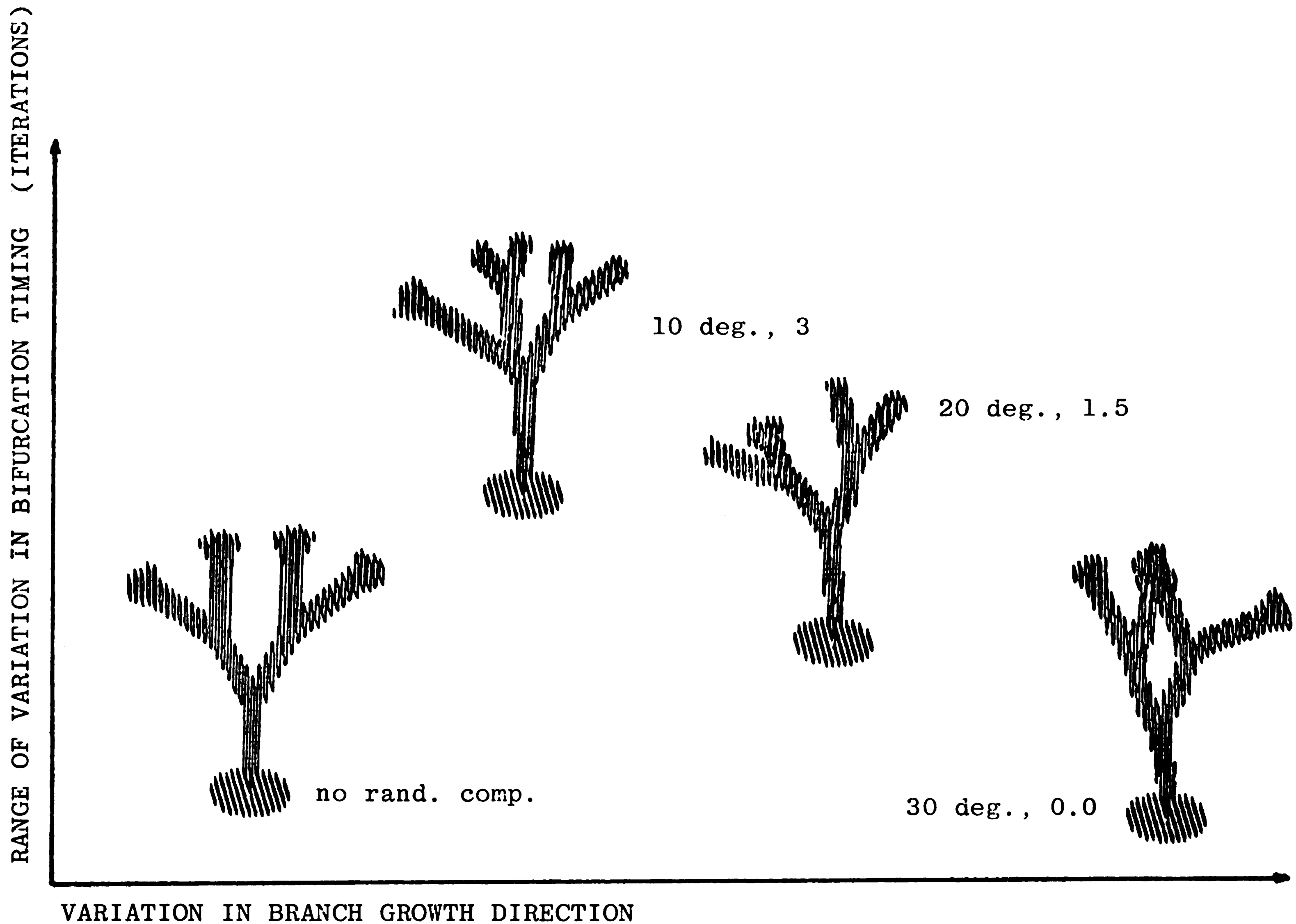


Figure 6a. Variability in branch growth direction vs. variability in bifurcation timing.

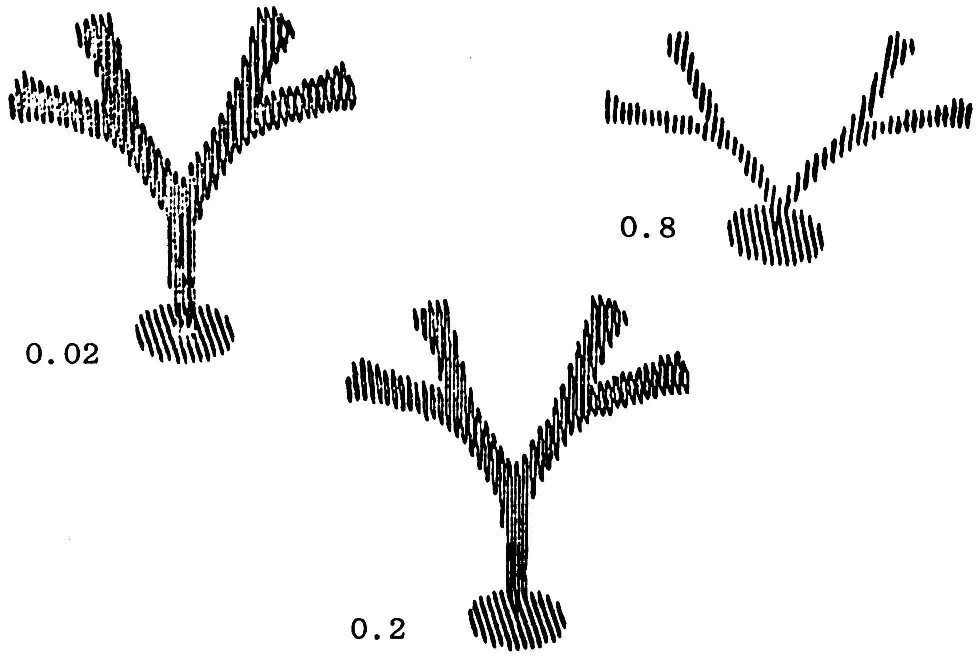


Figure 6b. The effect of different critical concentrations of endozone morphogen. The central figure has the standard critical concentration. The figure on the left has a lower critical concentration. It appears the same in later growth, but the early portions of the colony reached maximum width much earlier than the standard. The figure on the right had a high critical concentration. Notice the thinner branches and the nearness of the first bifurcation to the base, indicating that the endozone morphogen concentration didn't build up to the critical level until later in astogeny, thereby delaying the development of erect growth.

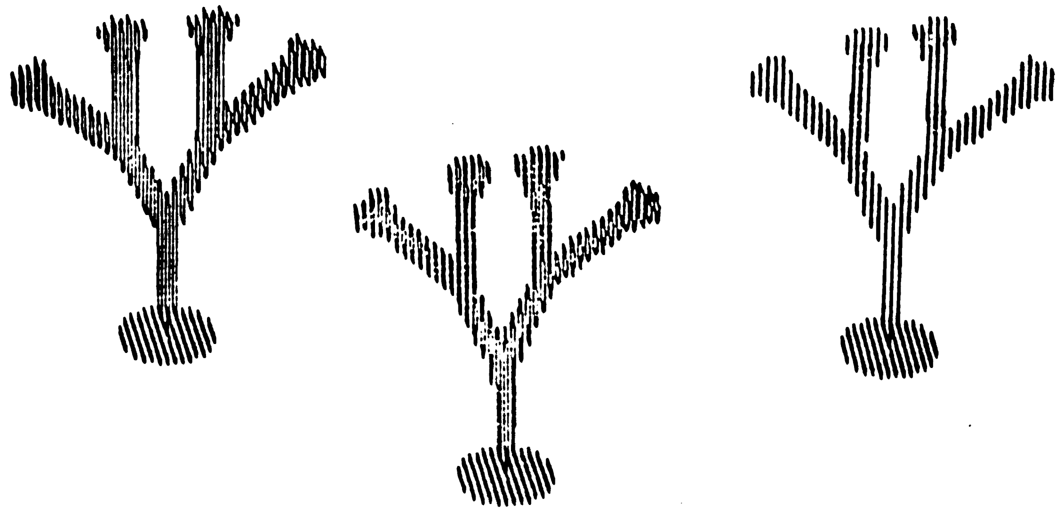

Figure 6c. The effect of endozone flattening. Due to non-isometric growth, or the effect of a mesotheca, the endozonal portions of a colony may be flattened. The figure on the left has cylindrical branches due to isometric growth around the branch axis. The central form is somewhat flattened because the growth rate of endozone is only 75 percent, in the "Y"-direction, of that in the "X"-direction. The figure on the right has ribbon-like branches with the "Y"-direction growth only 40 percent of that in the "X"-direction.

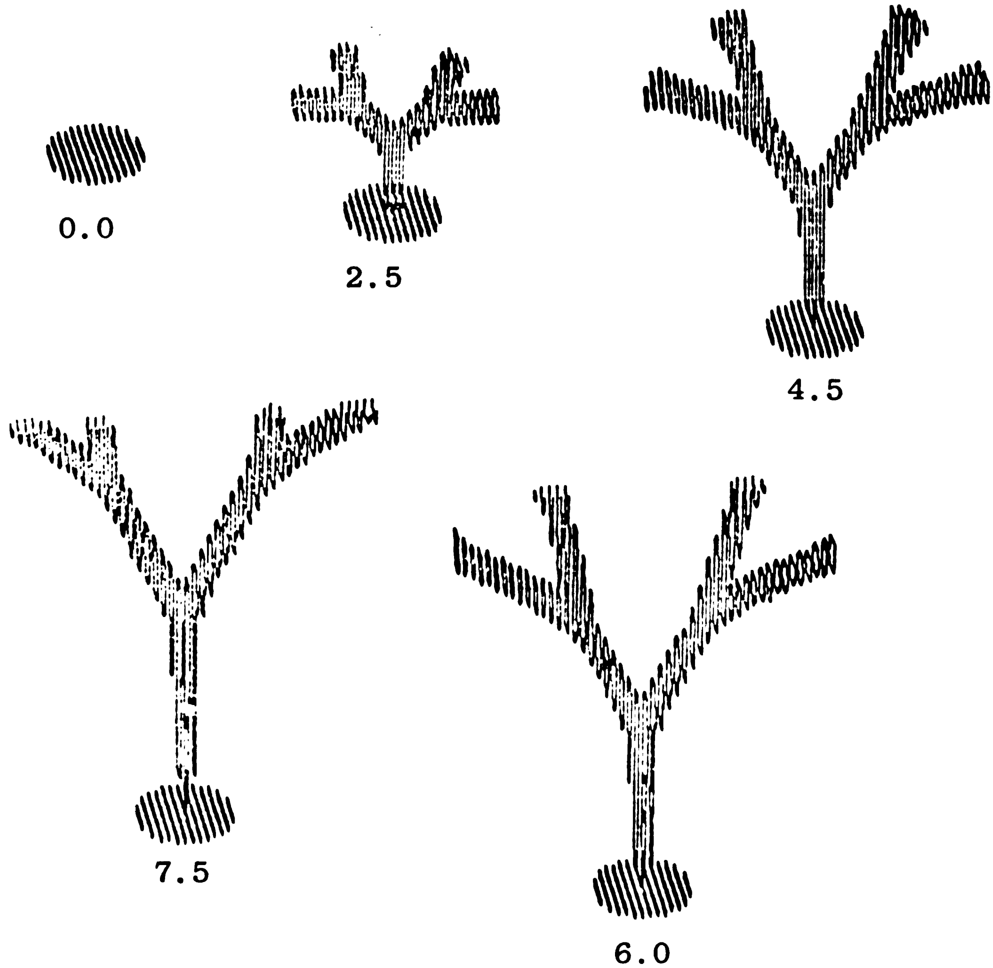


Figure 6d. The effect of different endozone extension rates. In these five figures, all parameters but the endozone extention rate are the same. Note that in the high growth rate figures, the workspace limits are reached and the plots are truncated.

and as such, adds potential heuristic value to simulations.

The width of the endozone, the mesotheca, and the shape of branch axes- To fairly great extent, the shape of the endozone of most double-walled colonies, especially those with low exozonal growth rates, determines the shape of the colony. Notice the columns in Figure 7, illustrating the proximal portions of colonies with different endozonal shapes and varying rates of exozonal growth. The top row is of particular interest because it shows (arising out of encrusting bases) only endozones, devoid of exozone, with varying amounts of tapering in the proximal direction. This indicates that in the earlier stages of the simulated astogeny the endozones were narrower than in later times. Empirical studies show this to be a common and widespread phenomenon in double-walled stenolaemates. Blake (1976) and Tavener-Smith (1974) illustrated this for some of the Rhabdomesita. Boardman et al. (1970) and McKinney (1977) indicate that it occurs in the Trepostomina. Bassler (1953) figures many examples of proximally tapering endozones and bases in the Trepostomina, Ptilodictyita, Rhabdomesita (including the family Arthrostylidae), and some families of the Cyclostomata. It is reasonable to conclude that when the endozone is first initiated it takes a considerable amount of time, in many cases, before it reaches its full diameter. It may be assumed that the skeleton-forming tissues anywhere is the colony potentially

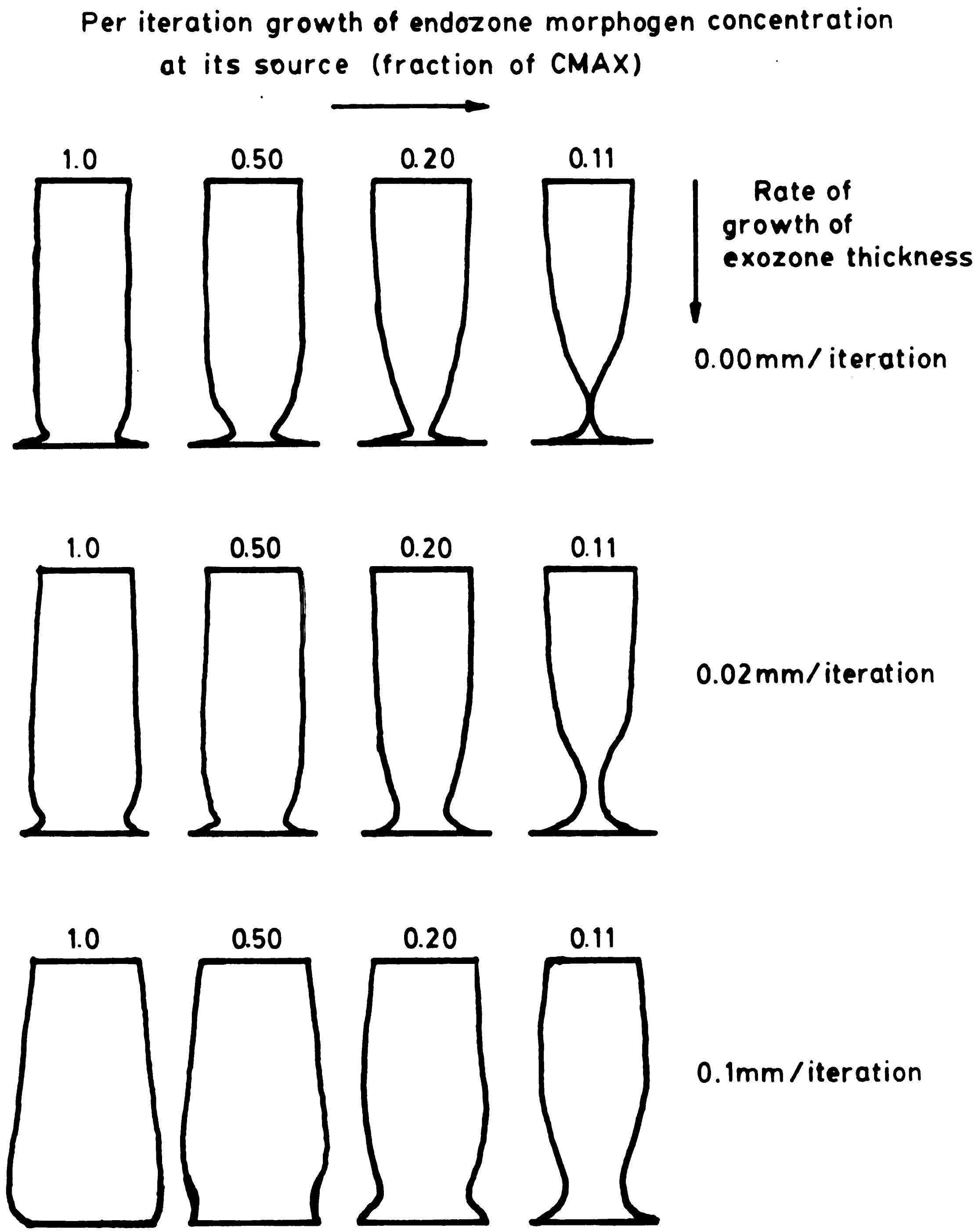


Figure 7. Some factors affecting the shape of the proximal portions of an erect stem.

are capable of producing either exozone or endozone. This is most simply modelled by having an endozone morphogen produced in the tissues at the tip of a branch axis and having it diffuse through the hypostegal coelom into the surrounding skeleton secreting tissues. There it induces endozone production and leaves those tissues outside its influence to produce exozone. The generally more dynamic activity in the branch tip bespeaks of such a mechanism. Anstey et al. (1976), after studying morphologic gradients in budding centers (called monticules) of the massive, encrusting trepstome *Amplexopora filiasa*, suggest these gradients were maintained by a substance diffusing from zooids in the centers of monticular areas. Podell and Anstey (1979) further this idea with evidence from other trepstomes. Urbanek (1973) suggested the diffusion of a morphogen to explain morphological gradients in graptolites. Bonner (1974) suggested several mechanisms of controlling patterns of growth, including active transport, polar permeability, electrophoresis, cell migration, and tropism. Diffusion is chosen because it seems the best suited, in that its implementation would require, in the case presented here for double-walled bryozoans, the least number of ad hoc explanations. On the other hand, the communication pores in the single-walled bryozoans (those which have them) are plugged with tissue, suggesting active transport may be more applicable to them because a diffusion model would require passing through membranes, which would probably restrict the range of the substance where membranes vary in thickness and orientation. There is also evidence of polarity in the communication pores of the Cheilostomida (Pyxibryozoa) (Boardman and Cheetham 1973),

Wolpert (1978), in a study of the epigenetic mechanisms in tetrapod limb buds suggests a way that undifferentiated cells may find their position in a developing limb by using a diffusion gradient. This situation is analogous to the conditions on a growing bryozoan branch tip. Wolpert suggests a steady state diffusion gradient that begins at a "source," where the concentration is the highest, and ends at a "sink," where the substance is destroyed, neutralized, or otherwise removed. Figures 8a,b contrast diffusion of a limited amount of substance and steady state diffusion. Both figures show the concentration as a fraction of the concentration at the source at time zero. The curves show the concentration distribution with distance from the source for several units of time after time zero. Notice in Figure 8a, that in the diffusion of a limited amount of substance, the concentration at the source becomes less through time, approaching zero at time infinity. Notice in Figure 8b, that in steady state diffusion, the source

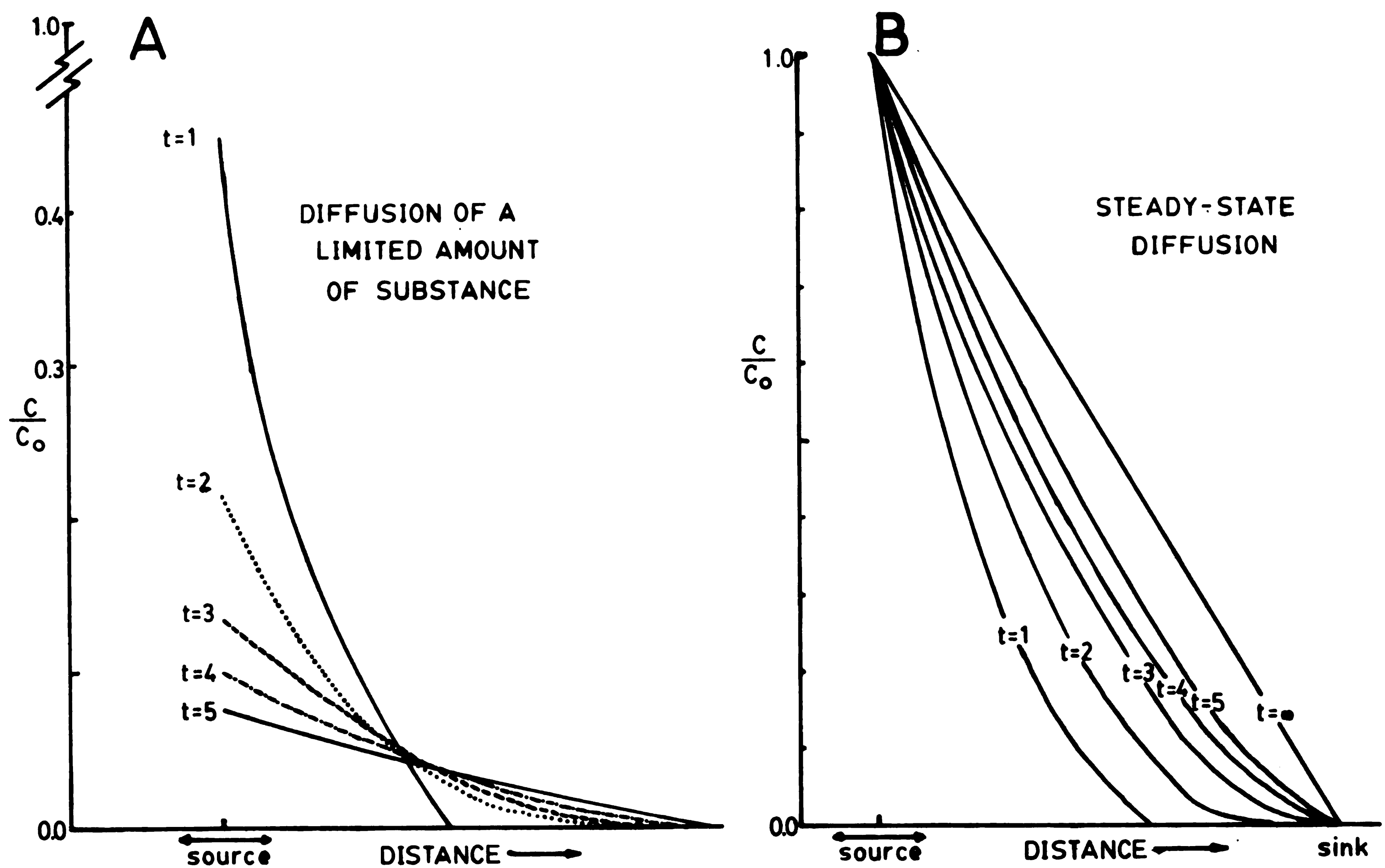


Figure 8. Two types of diffusion.

continually produces substance and maintains a constant concentration. Notice also that, as time goes by, the substance advances to the sink, but cannot pass. As time approaches infinity, the concentration at a certain point becomes directly proportional to its position between the source and the sink. Wolpert suggests that position of the sink may be determined by another, previous morphogen gradient that establishes both the source and the sink. Other possibilities, applicable to this study, are that the morphogen is unstable and breaks down over time as it gains distance from the source or that mature feeding zooids (or some other older tissues), a certain distance from the area of new growth, make a substance that neutralizes the morphogen. After the steady-state diffusion gradient is established, in Wolpert's model, the cells, which behave differently at different concentrations of the morphogen, begin to develop according to their position in the gradient. In this, they exhibit threshold effects. That is, above a certain critical concentration, they show one set of behaviors and below it another. Figure 9 shows the identical concentration distributions as in Figure 8b, but has, superimposed on it, two examples of hypothetical critical concentrations. Notice that the endozone is wider in the same morphogen gradient if there is a lower critical concentration and is narrower with a higher critical

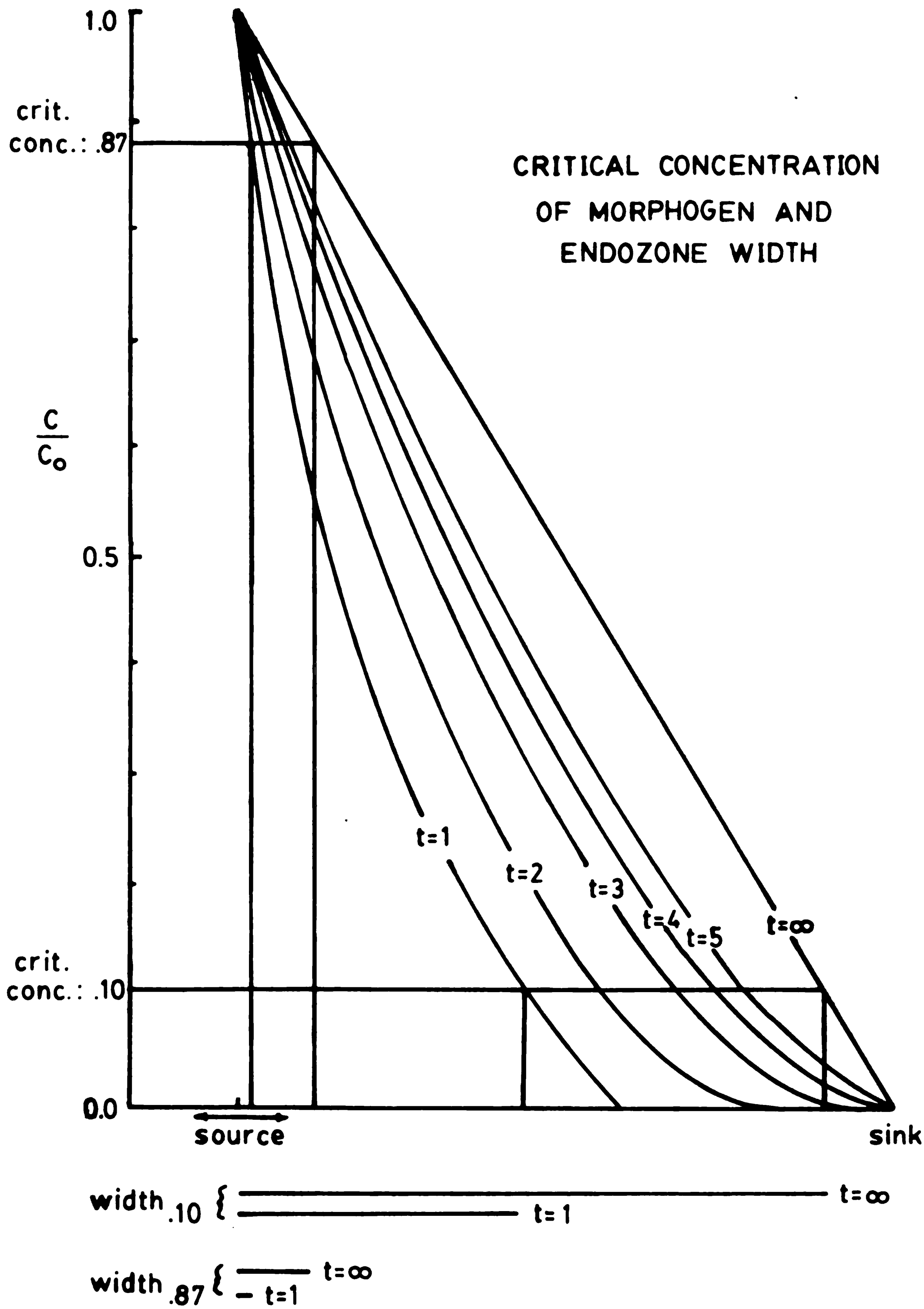


Figure 9. Two examples of hypothetical critical concentration superimposed on steady-state diffusion curves and the resultant endozone widths.

concentration. Figure 6b shows the effect of different critical concentrations in the simulations of different colonies. Notice that the endozone would be narrower if it were growing before the steady state was achieved, and continue to widen out until that time, but remain constant afterwards. This would explain the proximally tapered endozones except that the steady state is reached so quickly in the very short distances involved, and "time infinity" is probably a matter of minutes for most hormonal substances at this scale. Even the smallest erect colonies must have taken at least a few days to grow. A likely alternative is that the maximum level of production of morphogen by the source was limited by the size of the colony. Smaller colonies with fewer feeding zooids could probably not generate sufficiently large energy reserves to maintain the maximum rate of morphogen production. Adventitious branches, growing out of injured colonies illustrated by Blake (1976), having tapered bases where they are attached to the main stem, give additional support to this model. For this reason, the simulation starts its first axis with an initial morphogen source concentration of zero and it builds up to a maximum, at a constant rate through the first few iterations. (See Table 1, for the parameters involved.)

The first row in Figure 7 shows the outlines of proximal portions of the endozones of four hypothetical colonies grown for five iterations, where the maximum amount of morphogen production, the critical concentration, the distance to the sink, and the endozone extension rate are all constant, and per iteration growth rate of the morphogen concentration at its source is varied. Notice that as the morphogen source concentration growth rate decreases, to the right of the chart, it takes longer for the maximum rate to be reached and as a result the proximal portion of the endozone tapers more gradually. All of these simulated endozones are circular in transverse section as would be expected of endozone produced by tracking a diffusion pattern.

In many bryozoans, the upright portions of the colony are not nearly circular in transverse section. Many are seen to flatten prior to branching. This can be explained in the general model presented by the bifurcation of the endozone morphogen sources. Figure 10 shows the transverse outlines of a bifurcating endozone on the left, and its corresponding morphogen concentration distributions on the right, with point source(s), zero concentration indicator line, critical concentration indicator line, and brackets marking the width of the endozone in the plane of bifurcation. Time one, before bifurcation, shows a circular endozone. Time five, after the completion of bifurcation, shows the two separate nearly round endozones of two new branches. Notice that in time five the morphogen

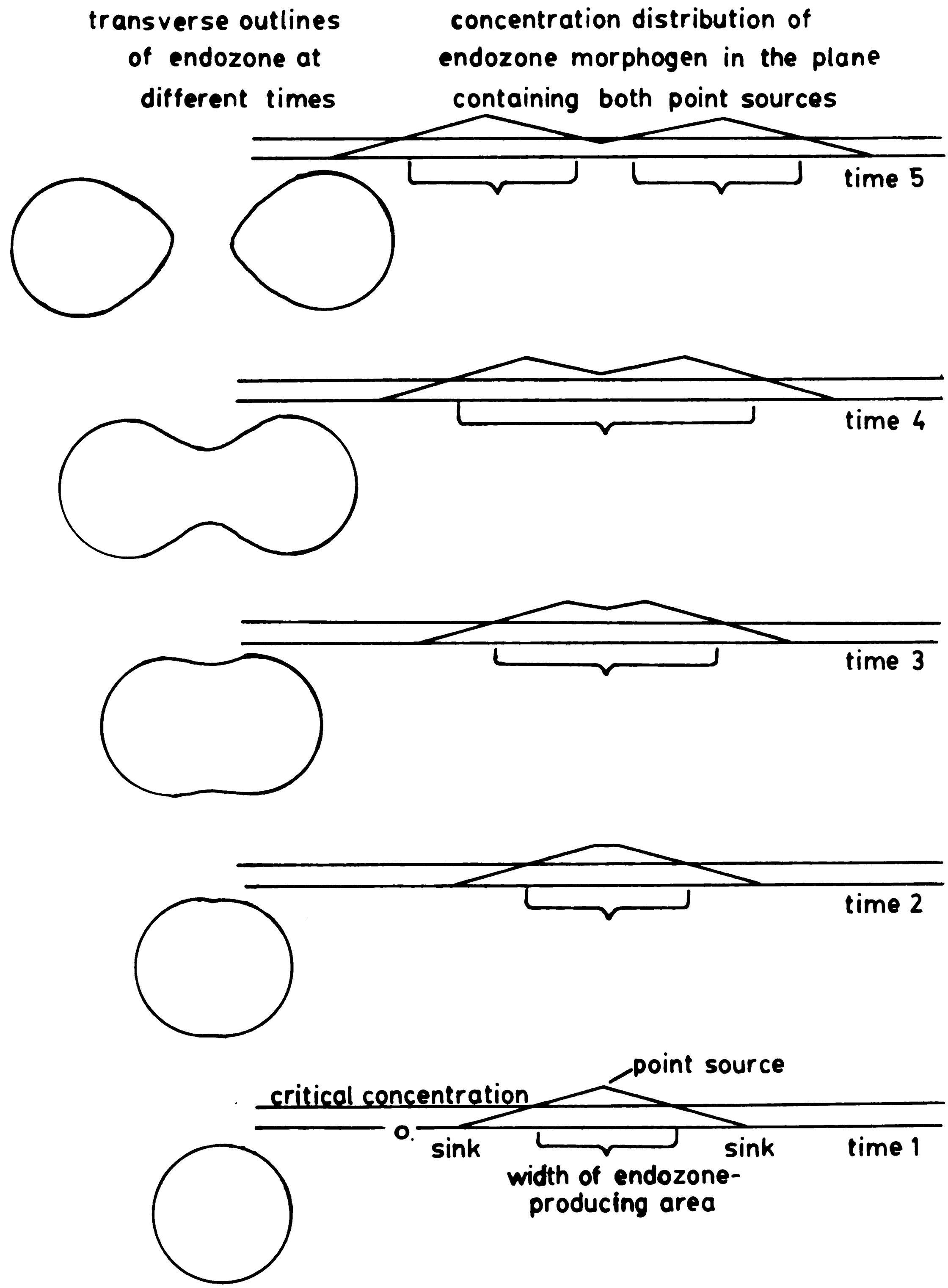


Figure 10. The effect of bifurcating the morphogen source on the shape of the endozone.

concentration distributions overlap even though the branches are already starting to separate. This is because the sources are far enough apart for the concentration level between them to drop below the critical concentration. Thus, the skeleton-producing tissues between the two new branch axes have passed beyond the lower threshold and now produce exozone, thus allowing the two sources to go off separately, growing in their new directions. An interesting situation appears if, through some mechanism, such as close-packing due to very slow growth, frequent morphogen source bifurcation, or very strong morphogen fields, the morphogen sources are constrained to stop diverging at the point illustrated by time three in Figure 10. If subsequent source bifurcation occurred, rather complex and massive endozones might be formed and depending on the planes of bifurcation some unusual shapes might be produced as seen in transverse section. In light of this, a detailed study of budding centers and their bifurcation patterns in the suborder Trepostomina (see Figures 18 and 19 for some proposed models) may be fruitful. Another way in which double-walled bryozoans produce non-cylindrical endozones is illustrated in Figure 11.

The bifoliate habit, most prominent in the Ptilodictyita, is characterized by the presence of a mesotheca, which is formed within a fold of epithelium drawn

Figure 11. Transverse sections illustrating cylindrical, bifoliate, and bipartite growth habits in double-walled bryozoans. Drawings at approximately 20x natural size.

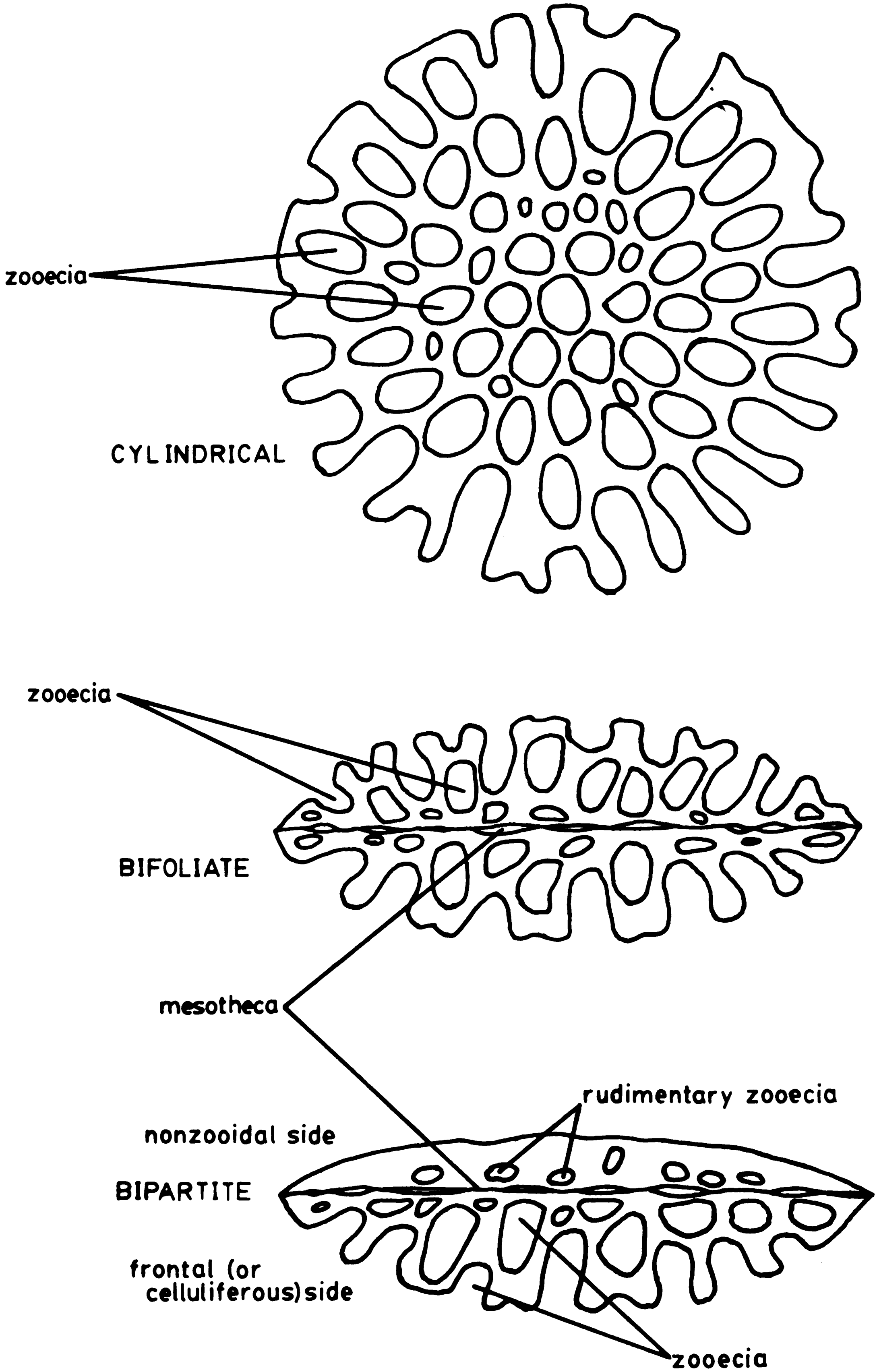
zooecia
CYLINDRICAL
zooecia
BIFOLIATE
mesotheca
rudimentary zooecia
nonzooidal side
BIPARTITE
frontal (or
celluliferous) side
zooecia

Figure 11.

up from the inner side of an already partly calcified basal lamina of bipartite colonies (such as Pseudohornera and Phylloporina) and the primary branch skeleton of the Fenestrina (Tavener-Smith 1975; Elias and Condra 1957). Studies made on the median lamina of Peronopora, a trepostome, list no significant difference between it and the mesotheca of the Ptilodictyita (see Tavener-Smith and Williams 1972; and Cumings 1912). The effect of the mesotheca is to flatten the colony, producing ribbon-like fronds with zooecial aperatures protruding from both sides. The bipartite habit is a modification of this (Tavener-Smith 1975) where the zooids on one side, named the reverse, are rudimentary. The effect of the median lamina is taken as a physical constraint in the development of a colony and its effect is modelled deterministically in the simulation. Parameters are read that relate the degree of flattening due to the presence of the mesotheca and the endozonal transverse section is simulated by an ellipse, flattened in the Y-direction. Figure 6c shows a series of simulated bryozoans exhibiting varying degrees of flattening of the endozone.

Some auxiliary growth habits- Now that the basic principles in the simulation have been discussed, there remains the question of continued growth and the problems it brings.

The first and most important of these is dichotomy. Few bryozoans that venture into the erect habit are content to remain as pillars. Branching can help increase surface area relative to materials and energy cost, help fill space more quickly, provide a framework for more efficiently filtering water and possibly increase larval dispersal potential. There are two main types of bifurcations in the Bryozoa: the symmetrical dichotomy and the production of side branches. They would appear to be the ends of a continuum, and in most cases, they are. However sometimes, most likely in stressed situations, adventitious branches occur. They may be seen to arise from endozone or near the endozonal portions of the branch tips as normal branches do, but at an unusually late time (Taylor 1978) or from exozonal areas such as monticules (Blake 1976). These adventitious branches are always part of asymmetric bifurcations, usually arising at right angles to the main stem. In some groups, such as the Acanthocladiidae, Arthrostylidae, and Cytididae, colonies are known to produce a fairly straight stem that gives off opposite or nearly opposite pairs of side branches.

In the simulation, bifurcation events are treated as being basically symmetrical, but freedoms are built into the system that would allow asymmetry. Adventitious branches are not considered in this study. The angle of bifurcation is input as a parameter, but because the growth vectors of the new branches may be modified before any growth occurs (via a random component or avoidance mechanism, see Figure 4), there is a good deal of freedom in this variable. The plane of bifurcation is taken as usually being parallel to or coincident with the XZ-plane, but it may be altered to some degree also.

The method used in simulating branch growth in DWBBF is illustrated in Appendix II. The growth vector is three-dimensional and has a magnitude equal to the per iteration endozone extension rate. Figure 6d shows the effect of different endozone extension rates in different simulated colonies. This vector, the position of the branch's tip, and the width of its endozone are included in the state variables of any one branch. (See Table 1.) These are the variables used in extending branch segments. The new branch is a cylinder with an elliptical (or circular, if there is no mesotheca) transverse section. The growth vector is its directrix. The simulation proceeds in this way, extending branches, bifurcating, and extending new branches as it fills the storage workspace. Of course, "filling space" assumes that there is space to fill.

If the simulation is extensive enough, eventually the growing paths of two branches will cross. When this happens in nature, the branches anastomose (unless they stop growing or have some other device to handle this contingency). There are two basic types of anastomosis.

The first is precisely determined and probably highly functional. It is best developed in the Fenestrina and certain of the Cheilostomida (Pyxibryozoa). Perhaps it reaches its highest development in a genus appropriately named Anastomopora (in the family Phylloporinidae), in which the anastomoses are so regular that the fenestrules, or holes in the meshwork formed by them, line up in straight, diagonal rows. This type of anastomosis, because of its very limited applicability, was not considered in this study. The other type is the incidental anastomosis (which, of course, can still be functional). There are two degrees of incidental anastomosis. The first is exozonal and is apparently where two branches, being widened by exozonal growth, come into contact and fuse together. This is common in the Trepostomina, where exozonal growth is extensive and colonies seem to have long duration, as is evidenced by their characteristically large size. The secondary accretions to the outline of fenestrate skeletons also cause this manner of after-the-fact anastomosis. The second form of incidental anastomosis is endozonal. Here a growing branch will run directly into another branch or colony part. This is also common in the Trepostomina where it would seem that the large size and ponderous branches either are more conducive to being run into or have more growth "momentum" and cannot easily avoid an oncoming anastomosis.

For colonies constrained to grow in a plane, anastomoses present a problem. This problem applies to any growth form whose feeding currents would be blocked or in any way altered or depleted by the presence of other colony parts, zooids, or other living surfaces on converging branches. This problem can be especially bad for extensive colonies. An analogy may be drawn to human urban dwellings. In order to have large populations living in a relatively small geographic area, larger buildings are constructed. But with more extensive domiciles come problems with ventilation, supplying needed utilities and services, waste removal, and overcrowding. Most bryozoans with extensive growth have evolved a wide variety of mechanisms to prevent incidental anastomoses. The need for these is shown in Figure 12, where an attempt is made to simulate an extensively branching colony without any such mechanisms. Clearly, in the jointed and other flexible bryozoans this is much less of a problem: the growing branches simply push one another aside and may overlap but because of the usual orientation (which by no means has to be vertical and on a level substrate) or surrounding currents, the zooids are separate. The Arthrostylidae are mainly jointed and have thin branches, having often as few as three or four zooids per transverse section. This gives a high curvature to the surface of the branch and prevents

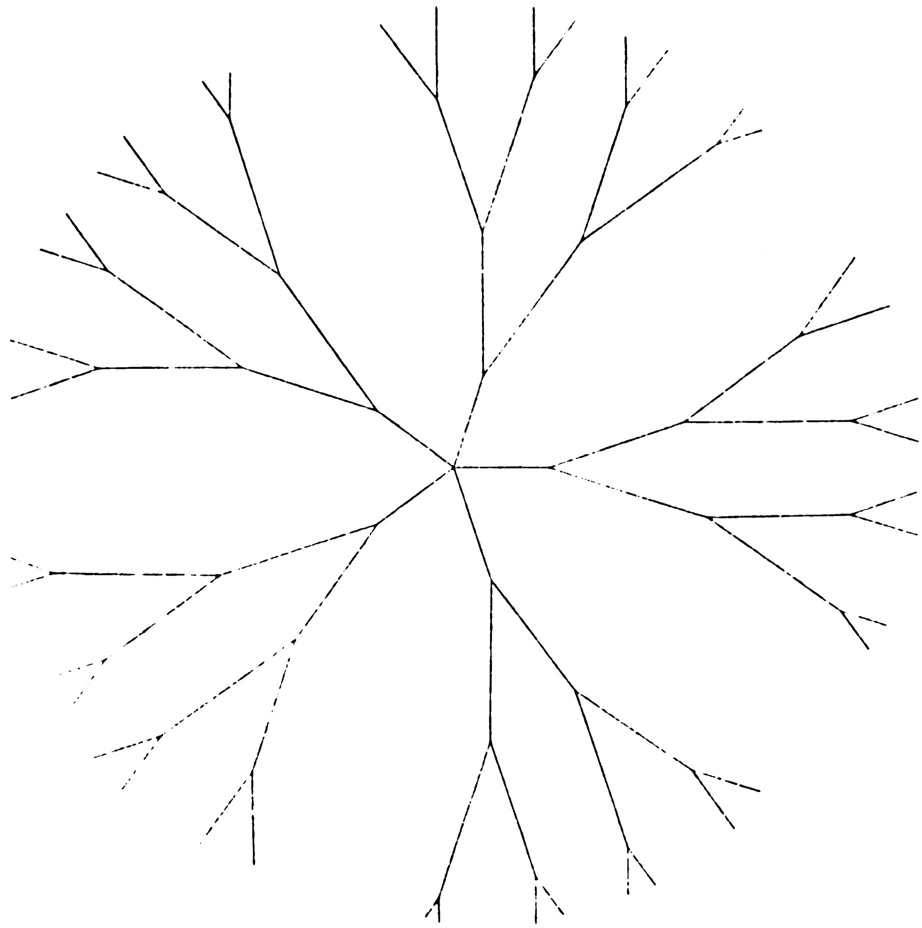

Figure 12. An extensive hypothetical colony without anti-anastomosis mechanisms. A single unit growth is about 3 mm here. Notice that although no anastomosis has yet occurred, intersection is imminent.

large areas from coming into close contact. Often zooids are restricted to certain portions of the branch as well.

Rigid bryozoans have to modify some aspects of their growth in order to prevent anastomosing. One solution is for the branch merely to stop growing when an anastomosis is imminent (Gardiner and Taylor 1980). If the colony is not too extensive, and there is a large random component to the growth direction, some limited avoidance might be maintained, for a few bifurcations, by random missing. Spirally arranged colonies may be able to delay anastomosing and overcrowding of branches the longest of any extensively branching type without resorting to other special mechanisms. They essentially have made their plane of bifurcation into a helical surface and allow one edge of the colony to function as the helical axis (McKinney 1980). Thus they can grow upward, sending out branches in a spiral manner, allowing them a large portion of arc in which to grow and bifurcate. However, even the branches produced by these curved-plane dichotomies will eventually begin to converge on one another if they continue through enough bifurcations. Gardiner and Taylor (1980) simulated their Stomatopora with alternatively constant, arithmetically decreasing or exponentially decreasing branch angles. However, this cannot go on forever, in that zooids may start to interfere with their sisters as well as their neighbors. Occasionally, studies of bryozoan forms that do much bifurcating in a single plane report that the frequency of bifurcations is lower in the distal portions of a frond (Elias and Condra 1957) or that a branch system traced distally shows longer periods of growth between bifurcation events distally than proximally (McKinney 1979, 1980; Tavener-Smith 1965). These are evidences of bifurcation inhibition. McKinney (1980) recognized a critical branching distance in Bugula turrita. If certain branch tips are too close together to branch without interfering, in some way, with the growth or life processes of one another, it would be best if they delayed bifurcation, even though one or both may be physiologically ready to do so. But, even this cooperative situation cannot last in its pure form although, intuitively, it seems that it might. The branches, no matter how carefully the branching angle is chosen beforehand and no matter how far away the inhibition effect acts, as early as the fourth or fifth bifurcation in a series, if there is just a slight random component, some of the branches will be converging (see Figure 13a). If there is no random component and the branches are constrained to grow in straight lines, parallel pairs of closely spaced branches, with wide spaces in between will develop as in Figure 13b.

It is conceivable that, in the Fenestrina branch convergence is prevented by the physical constraints of the dissepiments. It also seems likely that this effect,

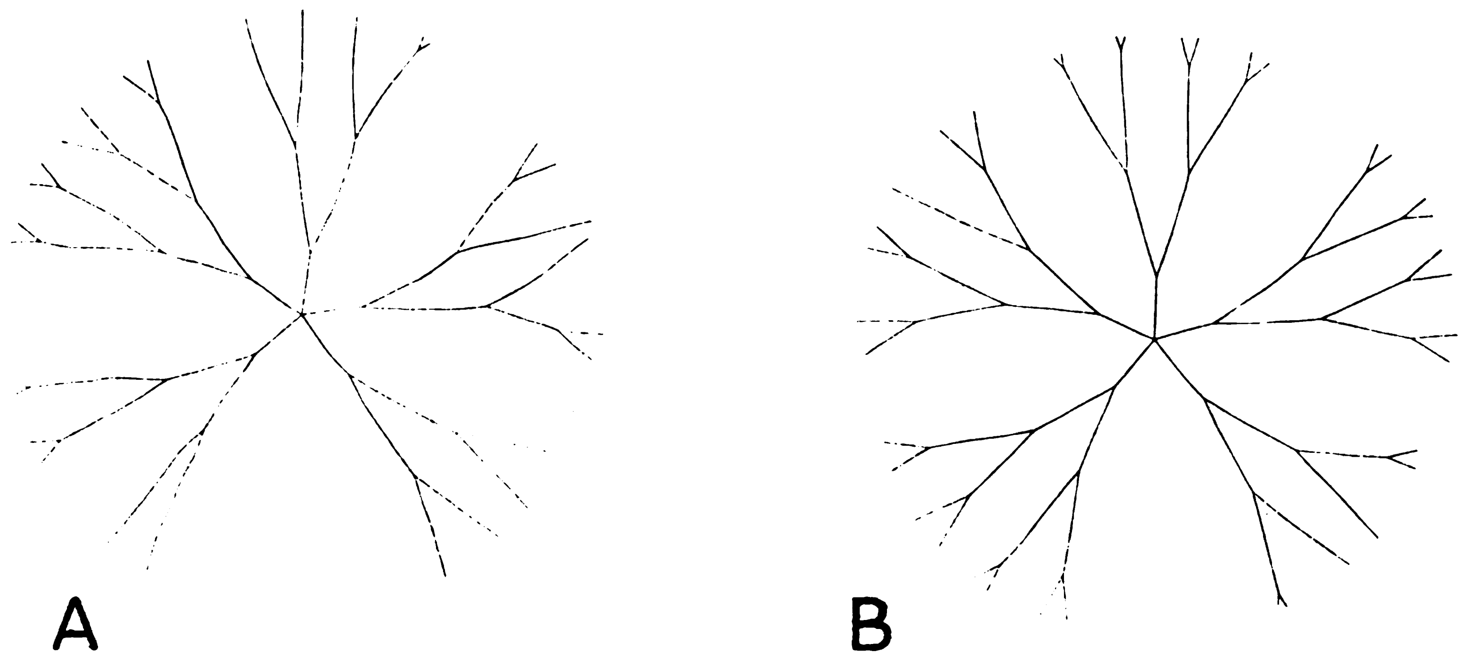


Figure 13. Extensive colonies with bifurcation inhibition but no auto-avoidance mechanisms. 13a exhibits a random component to branch growth direction. 13b has none.

plus a random component to the branch growth direction, which could then only operate on the side without dissepiments (which only applies to marginal branches) could account for the distal spreading of typical fronds of this suborder. However, this is still a mechanism operating beyond simple delay of bifurcation.

If branch growth directions are allowed to change slightly, but in a non-random manner to avoid the positions occupied by other colony parts, this convergence can be easily eliminated and a colony using both bifurcation inhibition and an avoidance mechanism could grow, in theory, to unlimited size without overcrowding or anastomoses. This applies to growth in three dimensions as well as two. Avoidance by itself is ultimately insufficient. With unlimited branching, the initially wide spaces between the branches would soon close. The avoidance phenomenon has been reported by authors, but seldom recognized as such. The decrease in branching angle in <u>Stomatopora</u> has been mentioned, recognized as important by many, and carefully measured (Lang 1905; Illies 1973; Taylor and Furness 1978). It has even been recognized that after a certain bifurcation the angle widens up again (Lang 1905; Illies 1973). But no one speculates as to a possible mechanism. In describing <u>Fenestella</u> <u>austini</u>, Elias and Condra (1957, p. 76) mention inflection in growing branches at certain critical times, "Branches straight to zigzag, turning at points of bifurcation, . . . . Usually neighboring branches assume zigzagging where bifurcating one after another within short space."

The extensive growth program, AASP, was initially conceived to deal with the problem of defining the avoidance mechanism and the way it may combine effects with other mechanisms, especially bifurcation inhibition and endozone extension rate in large, frond-like colonies (AASP stands for Auto-Avoidance Simulation Plotter). Figures 14a-d show a series of plots made by AASP. In this particular series the initial conditions are based on Cumings' (1904) description of the early colony growth of a bryozoan probably belonging to the genus Fenestrapora (although he called it Fenestella). He mentions a large vertical growth component, as the colony he described was initially developing into a cone-shaped net. But the simulation is two-dimensional and the main difference is that there is more area to occupy at first, in the simulation. After a brief early astogeny, Cumings' bryozoan developed five initial branch axes simultaneously (a characteristic of the Fenestrina is that there is highly specialized early astogeny). These branches grow out radially from the origin with equal amounts of arc between them and quickly bifurcate to form ten and so on. In the simulation, the growing tips bifurcate as soon as they are a certain distance removed from the other tips. Each

Figure 14. Extensive growth in colonies constrained to grow in two dimensions. The unit length is 2 mm in 14a-c, e, f, and 1 mm in 14d. Each plot shows the effects of the auto-avoidance mechanism and the branch-tip bifurcation inhibition mechanism. The values for these are as follows; a, CRDIST = 6., BFDIST = 6.; b, CRDIST = 12., BFDIST = 6.; c, CRDIST = 6., BFDIST = 3.; d, CRDIST = 12., BFDIST = 6.; e. CRDIST = 12, BFDIST = 6.; f, CRDIST = 12., BFDIST = 3. All simulations, except 14d (40 iterations), were run for 20 iterations and had 20 degrees of random variations in their branch growth directions.

The circle area shows the limits of the critical avoidance distance for one branch tip. The inset shows how the avoidance mechanisms's vector field is arranged. The lengths of each arrow reflects its relative contribution to the composite vector at the branch tip.

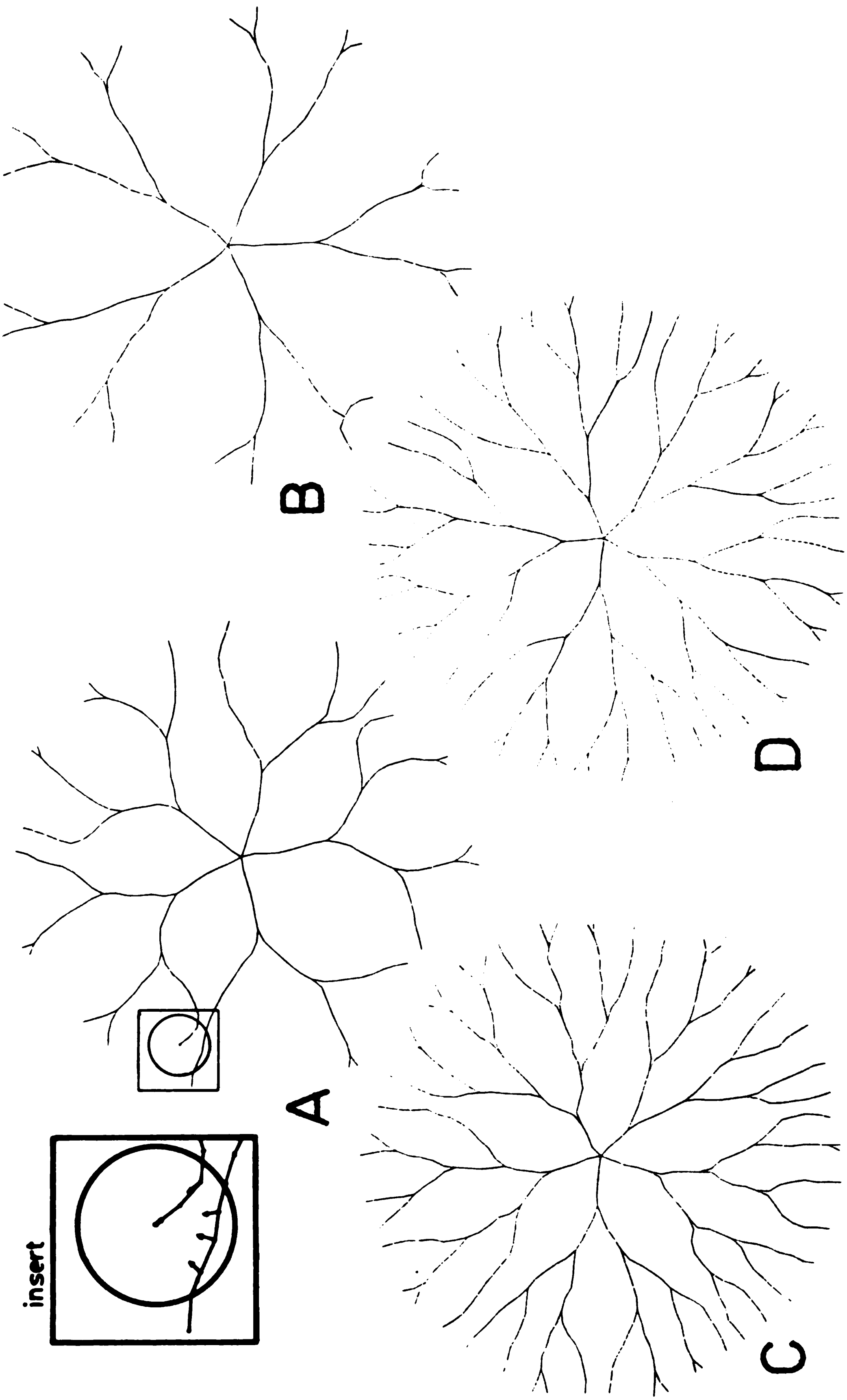


Figure 14.

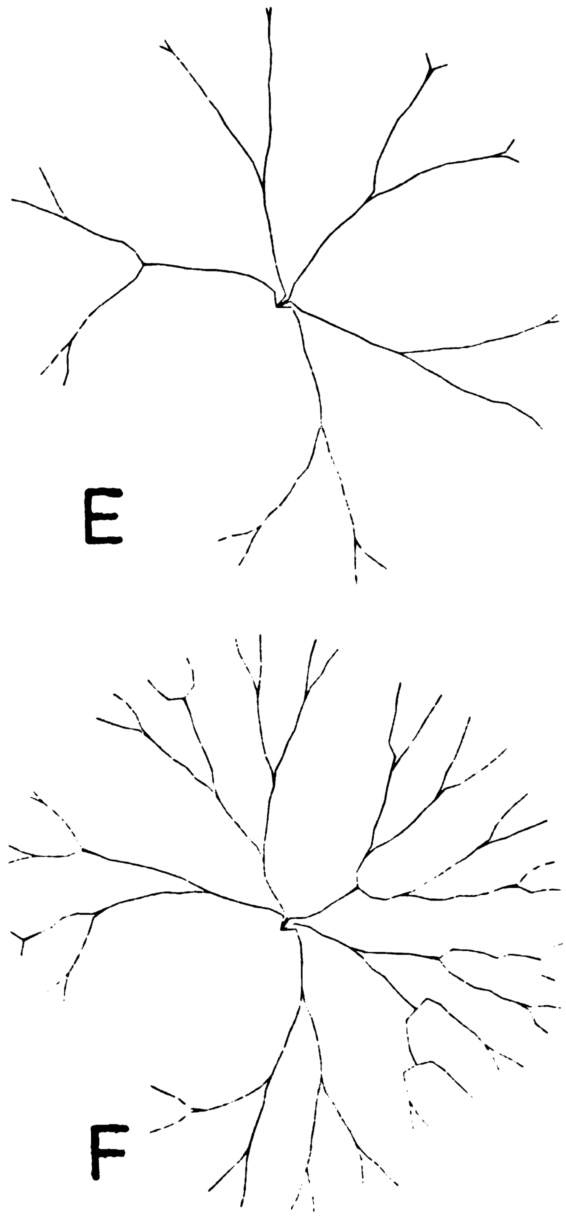


Figure 14. (cont'd.).

branch grows one unit segment at a time, incrementally. In each iteration, every tip is recorded to represent the position of that branch segment. This is so that a vector gradient may be constructed around a growing branch tip for the purpose of modifying the growth direction, using the avoidance mechanism (see Figure 14a, inset). Parts of the colony closer to a growing tip have a greater effect than those farther away. A critical distance is set, beyond which, a colony part will not be considered in the modification of a tip's growth direction. This is a matter of economy more than anything else. Ideally, all the other parts of the colony should have some effect, however small, on a growing tip. In short, the avoidance of each part of the colony by the tip can be represented as a vector, which summed with the other avoidance vectors of other colony parts, forms a composite vector which can modify the branch's direction of growth. There is also a random component to the growth direction which is important for founder effects, as mentioned earlier. Finally, the basic angle of bifurcation in this series is 180 degrees of arc, but the avoidance of the earlier grown portions of a tip's own branch greatly decreases this angle. This could explain the reduction of branching angle in the first few dichotomies of Stomatopora quite well.

Figure 14a illustrates the mechanisms described. Notice that the branches pinch and swell in exaggerated sinuous paths. This produces some asymmetrical bifurcations and large unoccupied areas. This pehonomenon is largely due to the initially great amounts of arc between the branches, large bifurcation inhibition distances, the coarse size of the unit increment, and the rather localized control of avoidance. Some straightness is produced in the branches by extending the basis of control by enlarging the critical avoidance distance as in the run shown in Figure 14b. Another mechanism, shown in Figure 14c, would be to decrease the distance at which the proximity of one branch may inhibit another. Notice here that the branches fill up the space more quickly and sinuosity is also reduced greatly. Some branches do come rather close together here, as the oscillations caused by the initially large arcs between branches are slow to damp at this increment size. Relatively even spacing is beginning to appear at the advancing edge, to the right. Comparing Figures 14c and 14d will show the effect of increment size on the damping of the initial oscillations. The run pictured in Figure 14d is identical to that shown in 14c except that the growth increment is half the size. Notice that even spacing of branches is achieved earlier in the advancing edge pictured on the right. Notice also, that the average spacing between branches approaches the bifurcation inhibition distance, indicating that it is the parameter which ultimately sets the spacing of branches. Furthermore, in that the bifurcation inhibition mechanism is part of the branch bifurcation timing mechanism, the results here concur with observations of real Fenestrina (McKinney 1980; Elias and Condra 1957, pg. 63). Figure 14e illustrates a run identical to that shown in Figure 14b except that the five initial branches are restricted, initially to eighty degrees of arc. It should be noted how the side branches curve around to fill space behind the initial wedge. Figure 14f shows a run that is essentially the same as in the 14e except that the bifurcation inhibition distance is less, allowing the more frequent bifurcation of branches. Notice how one of the margins of the colony has turned in behind the initial wedge in a spiral fashion due to a combination of the space filling behavior and the avoidance of parts of the other margin to the left of the field of view.

If one edge of the colony shown in Figure 14f could grow more quickly than the other and were free to grow into the vertical direction, it would pass over the other margin and continue to whirl its way over the rest of the colony, giving off branches in a radial manner that would develop into branch systems through bifurcations. This system would be nearly identical to McKinney's (1980) model for the general development of Bugula turrita and Archimedes. It should also be noted that Figures 14f and 14c differ only in their initial configuration. The right-hand side of Figure 14f shows the effect of this initially tight spacing on the growth direction oscillations. They damp out more quickly because they are less severe to begin with. Fairly uniform spacing is achieved much earlier in the advancing edge. These simulations are rather coarse for the Fenestrina because growth is very continuous in their net-like fronds. The best that can be hoped for is a crude demonstration of the basic principles of their early growth because the large increments used, in the simulations, exaggerate what would normally be minor inflections in the meshwork of a real colony. More success is achieved in the restricted arc simulations whose initial configuration duplicates the patterns of later growth stages, where the branches are beginning to grow in a more parallel fashion and slight inflections don't give rise to long-lived founder effects.

Finally, colonies with more discrete growth increments such as graptolites could be very precisely simulated by AASP. Bulman (1973, p. 18) illustrates some colonies of Clonograptus species that bear a remarkable resemblance to Figure 14d. In any case, regardless of the superficial exactness of the simulation, AASP has successfully fulfilled its originally intended purpose of demonstrating possible mechanisms for the production of pattern in extensively branching colonies.

After being developed for two dimensions in AASP, the branch-growth-modification-avoidance mechanism and the branch-tip-proximity-bifurcation-inhibitor mechanism were installed into DWBBF. Figure 15 shows the results of a run with a high avoidance effect. Without the avoidance effect the branches would all bifurcate in the XZ-plane, barring small deviations due to the random component, and produce a frond similar to the one shown in Figure 12. In Figure 15, initially small deviations brought about by the random component are changed into three-dimensional growth by the avoidance mechanism. It can be seen that the branch tips are all well spaced in Figure 15. The important thing here is that by utilizing this mechanism which, in two dimensions, serves to prevent anastomoses (and has some space-filling function on the margins of fronds), a serendipitous thing occurs. The model was free to move into the third dimension at any time, but it didn't need to until about the third bifurcation. So in avoiding anastomosis, three dimensional growth is produced, which, if it is referable back to real bryozoans, may constitute moving into a new adaptive zone. If this is true, then we have quite unexpectedly simulated a possible preadaptation. This should help to emphasize the value of geometrical flexibility in symbolic

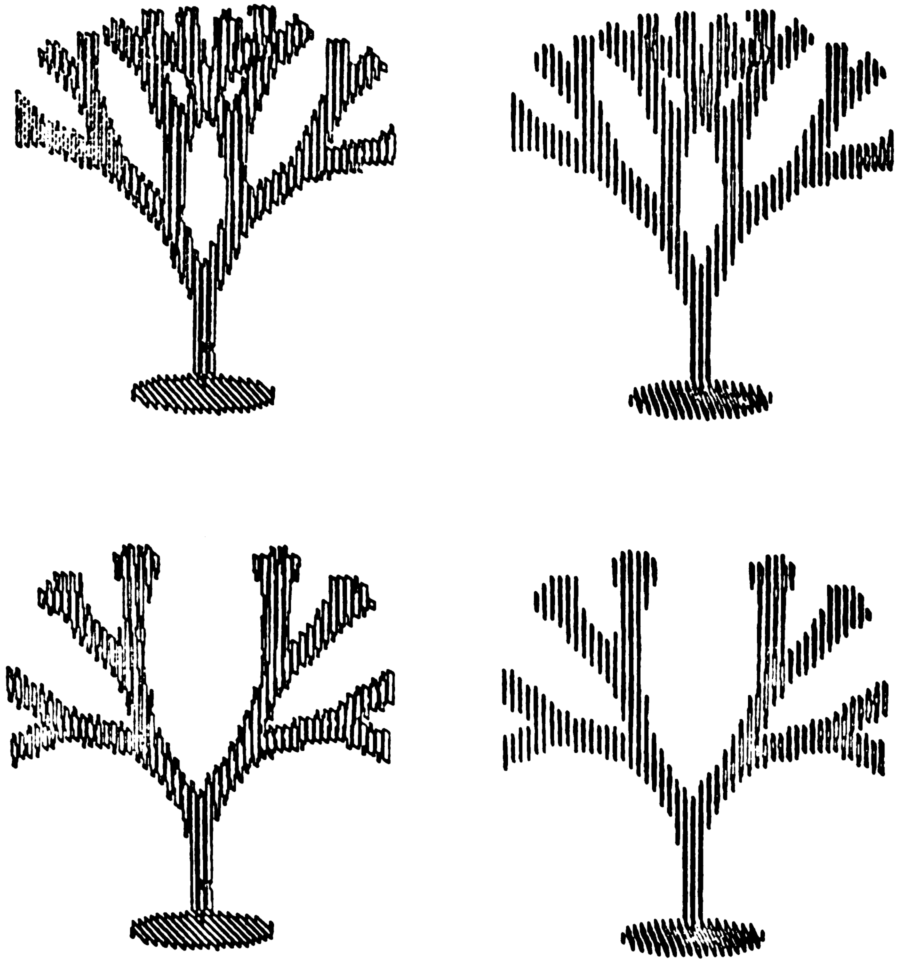

Figure 15. Extended growth with bifurcation inhibition and an auto-avoidance mechanism. These two sets of stereo pairs represent the results of two simulations with all parameters identical except that the run represented by the upper pair has no auto-avoidance mechanism and no bifurcation inhibition mechanism. The lower pair has both. Notice that the branches intersect in the same plane in the upper pair and that, in the lower pair, they actually turn out of the plane of bifurcation, initiating three-dimensional growth. Both simulations had little (5 degrees) of random variation in branch growth direction and none in bifuration timing.

simulations of ontogeny.

Still referring to Figure 15, notice that the planes of bifurcation are still lined up fairly well around the X-axis, until about the third bifurcation. This is due to the definition of the nature of bifurcation in bifoliate colonies, which are being simulated with the same algorithm. They bifurcate in the plane of the mesotheca, which is simulated as being aligned with the X-axis. However, in cylindrical-branched colonies, where this same type of branching pattern is common, there are no constraints from a mesotheca and that, if they do not easily and regularly change their planes of bifurcation, a special mechanism may be required to explain their behavior. This subparallel arrangement of bifurcation planes may be due to an ecophenotypic effect, that may be controlled by some environmental polarity, such as current direction. It may also be, in part, answered by budding pattern. Certain polarities are well known in budding patterns of the early astogenies of many byrozoans. Podell and Anstey (1979) show how these polarities are duplicated in monticules and to a lesser extent in branch axes. This subtle reminder of the original bilateral symmetry of the colony, along with the help of a certain amount of constructional intertia, and no mechanisms to alter the plane of bifurcation, may be all that is needed to keep the cylindrical byrozoans budding in a plane. Thus, inertia, which is very easily simulated and is often simulated unintentionally, or at least is taken for granted, may be a very important morphogenetic mechanism. It would appear that in simulations of ontogeny, with the purpose of analyzing morphogenetic mechanisms, it may be well to determine in which places in the algorithms used, inertia is being assumed.

Complete freedom in branching would also involve the freedom to rotate the plane of bifurcation into any orientation about the axis of the growth vector. Such a mechanism may be needed to properly simulate organisms which can branch, with equal facility, in any direction. Such a freedom could be easily produced using the system of bipolar spherical coordinates discussed earlier (see Figure 5). The growth direction of the parental axis is taken as the original vector and PHI PRIME is half the angle of bifurcation. THETA PRIME may be found using a vector gradient like the one used for the avoidance mechanism or taken at random from a normal distribution centered on the plane the vector makes with the X-axis.

Other auxiliary growth habits simulated but not analyzed include the basal common bud (see Figure 16) and exozonal growth (see Figure 17). (Other secondary thickening such as frontal budding, could be simulated in the same manner.)

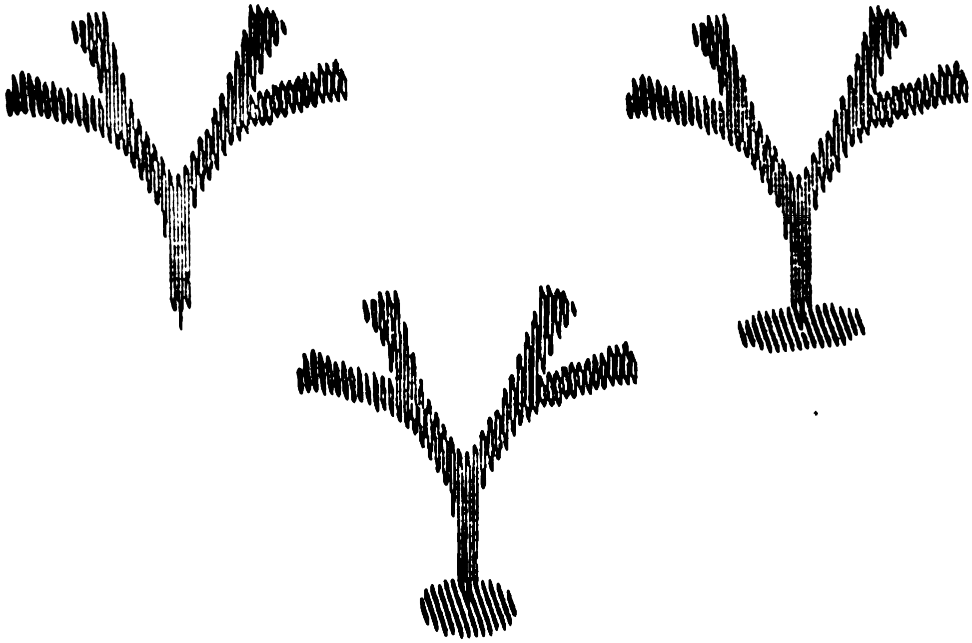

Figure 16. Simulation of the basal common bud. The figures show: no basal incrusting growth (left), equilateral incrustation (center), and incrustation in a preferred direction (right).

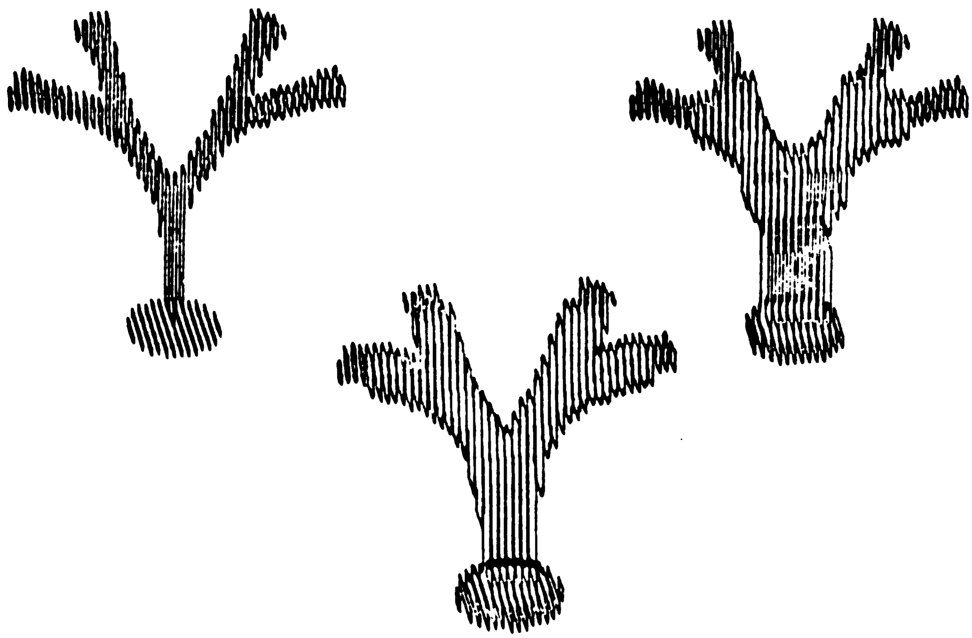

Figure 17. Variation in exozonal growth rates. There is little or no exozonal growth represented by the figure on the left. The exozone thickened at a rate of one unit per 5 iterations in the simulation represented by the figure in the center, and one unit per 3 iterations in that represented by the figure on the right.

Further mechanisms and possible simulations include allometric growth rates, various ecophenotypic effects, a randomized encrusting growth model, helical colonies, colonies with tightly packed sources of endozone morphogen resulting in coalesced axial endozones (Figure 18 shows a model for the growth of Amplexopora filiasa, based upon mechanisms developed in this simulation), and colonies with bundled endozone morphogen sources (see Figure 19, for a general model for erect trepostomes). Further simulations of specific sub-groups within the double-walled stenolaemates and simulations of various phenomena exhibited by the astogeny of these organisms are other possibilities.

Further studies of colonial organisms of reptant habit could be done using AASP and of colonies where zooid shape is important, using the modification of DWBBF called BBK. Further studies into the causes of spiral growth may be carried out using the ground work provided herein.

## DISCUSSION

This study has presented the importance of synergistic effects in the simulation of colony development and the value of built-in freedoms for the purpose of producing heuristic simulations. Table 1 summarizes the parameters and state vairables used in the simulation. The values in Table 1 represent independent simulations. Each is classified according to Harbaugh and Bonham-Carter

Figure 18. A model for the growth of *Amplexopora Filiasa*. Figures 18a-d represent a step-wise extension of the principles discussed for simple, erect forms to the more complex, massive *Amplexopora*. a, longitudinal section through a hypothetical simple double-walled colony. b, a similar colony exhibiting more frequent bifurcations, but with the same endozone morphogen distributions and critical concentrations. c, a colony with frequent bifurcation of branch tips (morphogen sources) where plane of bifurcation is freely changed and the tips, consequently, are in a close-packed arrangement in the living tissues surrounding the colony. Figured is a longitudinal section through a hemispherical colony. Note that the traces of some branch tips appear to end. This is where they pass out of the plane of section. For the sake of simplicity, no externally originated traces are shown entering the plane of section.

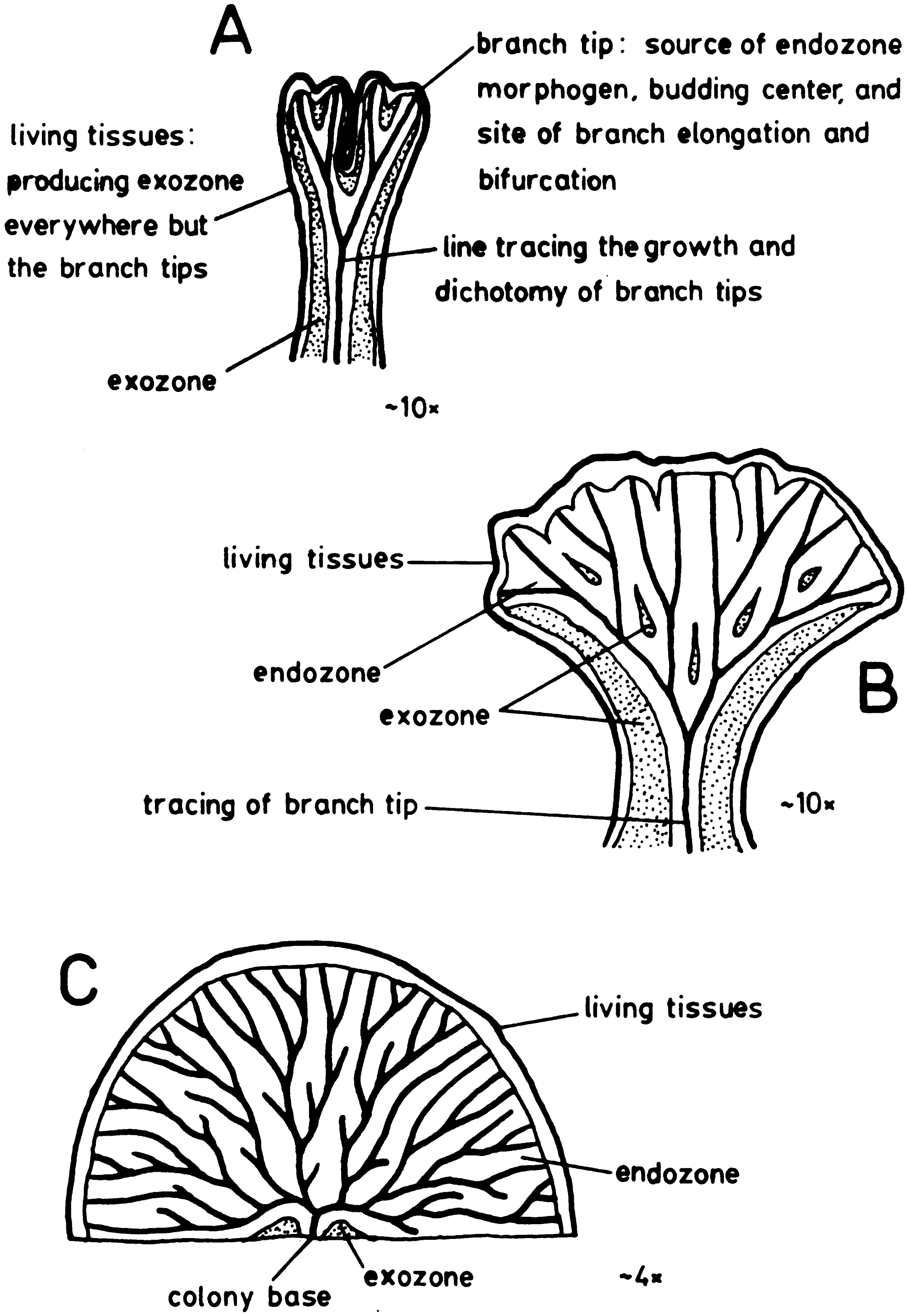
A
living tissues: producing exozone everywhere but the branch tips
branch tip: source of endozone morphogen, budding center, and site of branch elongation and bifurcation
line tracing the growth and dichotomy of branch tips
exozone
~10×
living tissues
endozone
exozone
B
tracing of branch tip
~10×
C
living tissues
endozone
colony base
exozone
~4×

Figure 18.

D

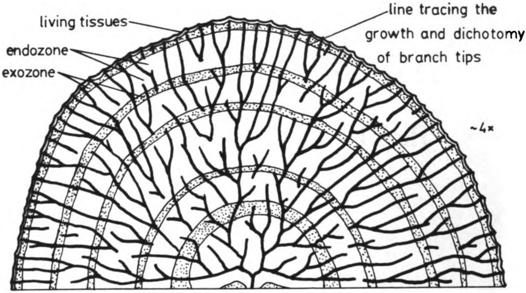


Figure 18. (con'd.). d, a longitudinal section through a colony very similar to the colony in c, but whose lfe extends through several growth cycles. Each cycle ends with the shutting down of the endozone-forming mechanism, explained in the model as the source concentration of the morphegen falling below the critical concentration. This allows a blanket of exozone to form. The next cycle begins with a colony-wide reactivation of morphogen production, causing a blanket of endozone to be accreted beneath the living tissues. Notice that the traces of the branch tips cross through the exozone, where they are manifest as raised areas known as monticles. These monticules are also present in the endozone of Amplexopora filiasa and, in longitudinal section, are the physical representation of the branch-tip traces figured above. Note that the branch axis traces move in and out of the plane of section due to the three dimensional nature of their pattern of growth. Compare the branch-tip traces with the longitudinal sections of endozonal monticules figured in Anstey et al. 1976.

Figure 19. A general trepostome astogenetic model. All drawings show a transparent view of part of a hypothetical bryozoan colony. Bumps in the outline, solid circles, and broken circles represent monticules in various aspects of viewing, profile, top view, and hidden, respectively. a, a small trepostome colony modelled after a colony of *Hallopora nodulosa*. b, the distal portion of a colony modelled after *Rhabdomeson*, a member of the order Cryptostomida. c, the distal portion of a colony modelled after *Nematopora*, also of the order Crypotostomida. d, a simplified drawing of the external form of a *Hallopora* colony showing freely varying branch growth directions and planes of bifurcation. e, a transparent view of a hypothetical trepostome colony modelled after a specimen of *Heterotrypa ulrichi*, showing the varying shape of endozone common in the suborder Trepostomina.

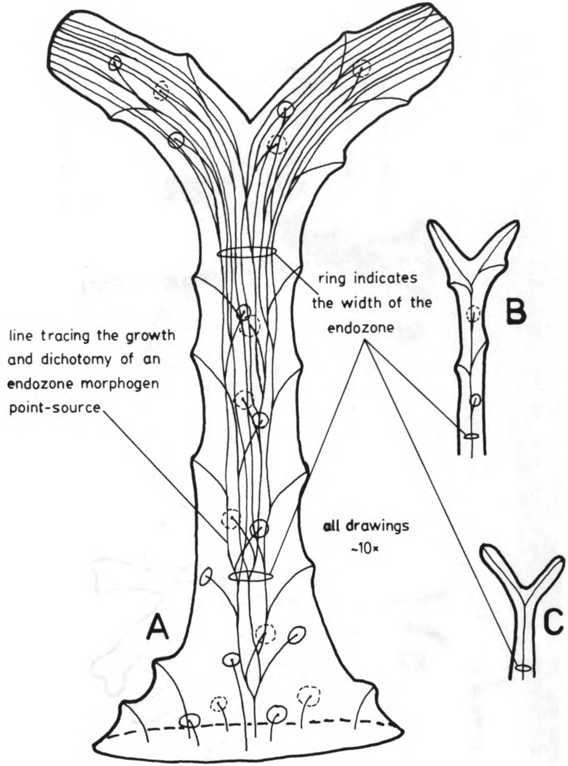
ring indicates
the width of the
endozone
line tracing the growth
and dichotomy of an
endozone morphogen
point-source
all drawings
~10×
A
B
C

Figure 19.

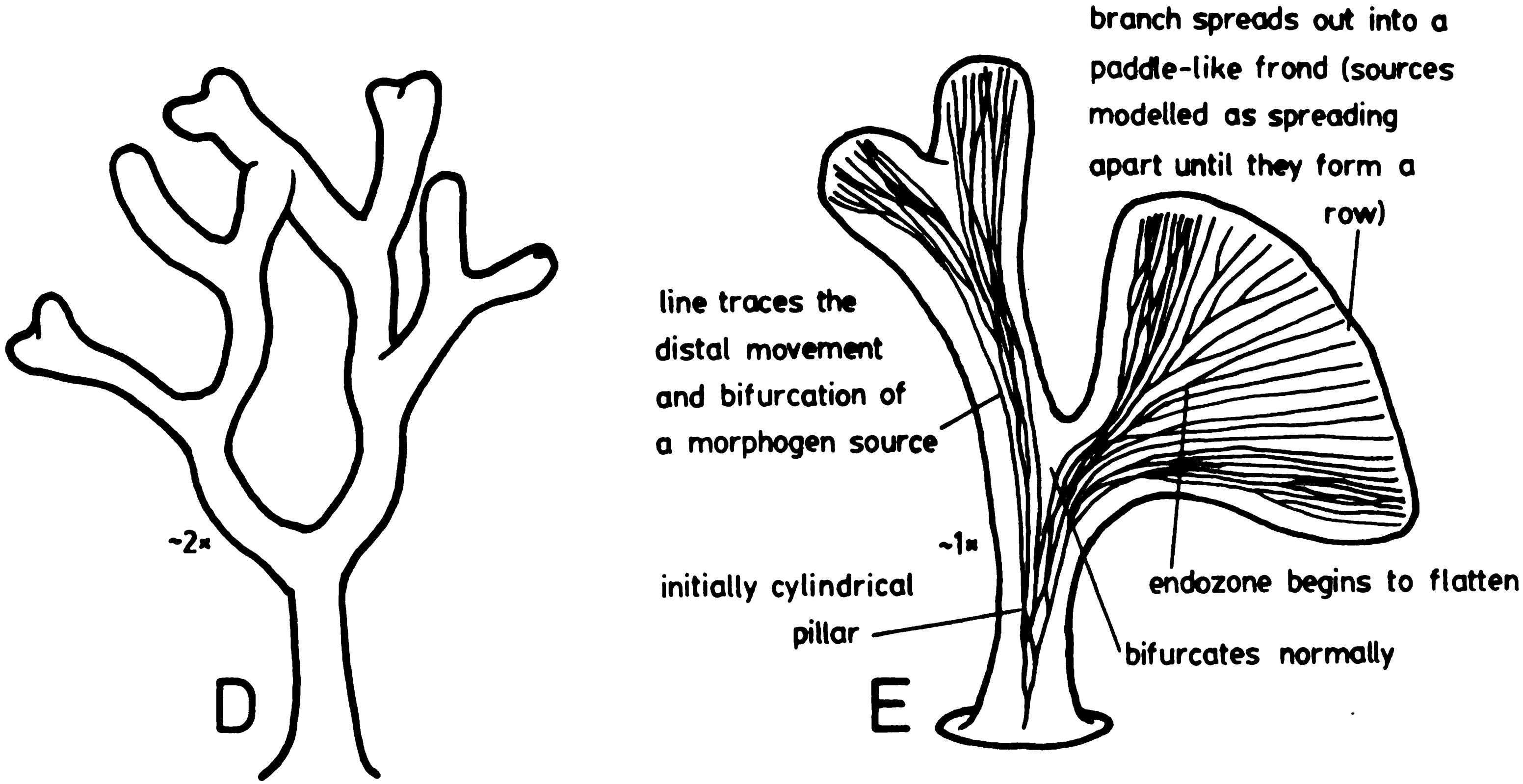


Figure 19. (cont'd.).

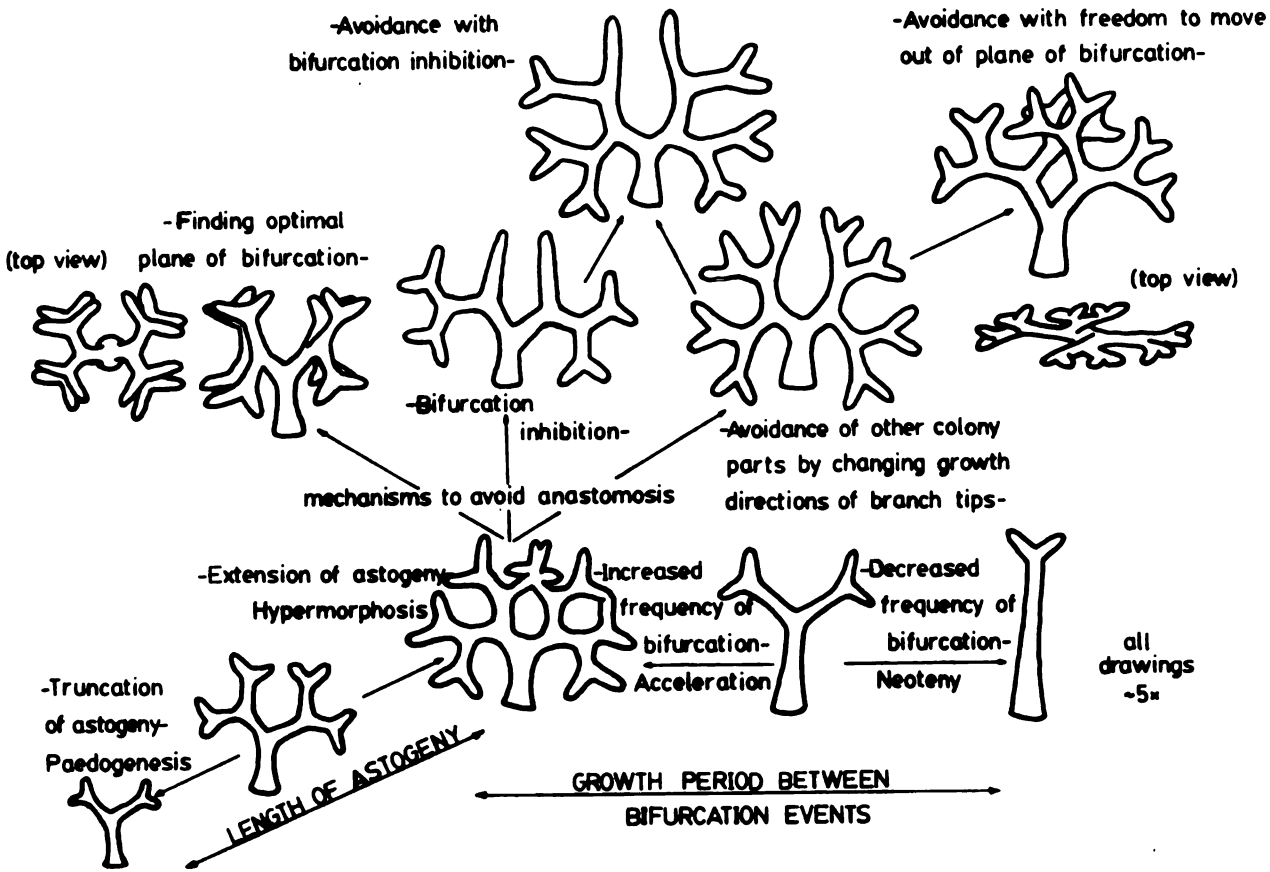


Figure 20. Heterochrony in astogeny and solutions to complexity problems arising from acceleration and hypermorphosis.

(1970). Parameters represent constraints to astogeny and can be phylogenetic, functional,fabricational, or a combination of these in nature (see Seilacher 1970; and Raup 1972). State variables are dynamic simulations that can be further elaborated or simplified. They represent the system being simulated, which can itself, be simplified by the removal of state variables or be made more complex by the addition of new ones. This study offers an example of the change of importance of certain state variables and parameters with changes in the complexity of the organism simulated and the level at which the simulation is examined. Both parameters and state variable may represent directly or indirectly measureable characteristics. Two state variables, independent of a third, may combine effects to produce another variable that is also independent. A researcher may then be able to consult Table 1 to determine the mechanisms that produce the characteristics he is measuring, if he wishes to determine their degree of independence.

One may also use the chart to find a pair of independent parameters or state variables that are measurable in a taxon under study and use them to construct adaptive landscapes. These will help determine the constructional morphological constraints on the group of organisms with respect to those parameters or variables (Raup 1967; McGhee 1980).

Because certain components of the skeletal growth mechanisms and the timing of astogenetic events can be simulated by random variables, the synergistic effect of many small and most likely ecophenotypic components is indicated. The absence or restriction of random variability in colony growth may indicate canalization of development during evolution from ancestors with a wider range of ecophenotypy. Other components of the simulation may reflect genetics or ecophenotypy or combinations of these. Ecophenotypic effects can be considered as those contributors to astogeny (or ontogeny) which, although programmed into an organism's genetics as possible developmental pathways, are responsive to environmental signals, perturbations, or irritations (e.g. flowering that is timed by photoperiod sensitivity, corals building stocker skeletons in more agitated water and more gracile forms in quiet water, or the development of pearls in oysters as a response to a sand grain trapped between the shell and the sensitive mantle). These effects can be distinguished from other morphological constraints in that they reflect the unique individual history of a particular organism as it affects the genetic (phylogenetic, functional and fabricational) aspects of the organism's construction. Ecophenotypic effects result rather from the deterministic responses of the developing organism to the various situations encountered during its ontogeny. In that these situations may be caused, in part, by various phenomena that can be grouped collectively into "random chance," the ecophenotypic effect may be thus related to the random component of development. However, it is important to note that the random component may operate at all levels of the organism's natural history, genetics, and individual and colonial development.

Some of the mechanisms developed in this study, such as the avoidance mechanism, which suppliment more widely accepted mechanisms, such as accretionary growth, and some of the phenomena predicted herein may provide material for future empirical research. Careful restudy of well preserved (especially complete) colonies will provide estimates for the parameters modelled in this study. For instance, statistical determinations of auto-avoidance and other fabricational mechanisms may be valuable for taxonomic purposes. There may be applications to the systematics of other colonial animals due to common problems. Certain evolutionary mechanisms having to do with coloniality may be discoverable only through the analysis of astogeny. Great potential exists for the study of heterochrony. Figure 20 shows how hypermorphosis and acceleration can lead to problems of complexity that can have a variety of solutions. In a computer simulation of heterochrony these processes could be manifested at any point in development, be run forward or backward to determine the most likely forms of descendants and ancestors. This will produce realistic evolutionary intermediates, allow for the formulation and testing of evolutionary hypotheses for various groups and taxonomic levels.

The approach followed in this study has been shown to produce not only relatively realistic simulations but also to have a high potential for serendipitious discovery. A realism therefore must be produced which approaches that of the physical simulations and yet the flexibility and potential for complexity of characteristic symbolic simulations.

APPENDICES

# APPENDICES

Here are listed the algorithms named in the text (APPENDIX I), descriptions of the derivation of the various geometrical coordinate transformations used to produce rotations of points and memory images (APPENDIX II), and a listing of some pseudo-random number generators that may be useful in the computer simulation of ontogeny and astogeny (APPENDIX III).

# APPENDIX I

## DWBBF

The programs used are listed here. The first, DWBBF, simulates various aspects of a double-walled bryozoan colony, including: endozone extension and width, the effect of the mesotheca, branch bifurcations, spacing, and timing, exozonal growth, and encrusting growth at the base of the colony. It produces colonies of limited size and complexity with usually less than twenty branches, and stores the growing memory image in a workspace that is filled as the run continues. When the iterations have been completed, a stereo pair of perspective drawings are plotted which represent, at a scaling factor of 1.0 (10-20 times the size of the bryozoan simulated), a pair of images as they would appear when viewed from a distance of 602. mm.

There are 6.0 degrees of rotation between the left and right images. This represents the angle of view between the average pair of eyes and a single image at that distance. For sharper lines, the images may be plotted at a higher magnification, up to 3.0 (30-60 times the size of the bryozoan simulated), and then photographically reduced.

The program is designed to run via the batch process and the input data must follow the program as a set of data cards. The program may be accessed interactively for the purpose of changing the input parameters and then submitting it to batch. There are two versions of the program available interactively, one with a 20x20x60 bit workspace located in the permanent file:

DOUBLEWALLEDBRYOZOANBATCHFILE20NP

and one with a 50x50x60 bit workspace located in the permanent file:

DOUBLEWALLEDBRYOZOANBATCHFILE50NP.

The programs are cataloged as "editor work files" and must be accessed using the "ATTACH" and "USE" commands. Changes to the data deck are best pursued after using the "SYSTEM, BATCH" command.

```
C*****************************************************************
C*     THE FOLLOWING PROGRAM IS DESIGNED TO RUN ON THE MICHIGAN   *
C* STATE UNIVERSITY COMPUTER SYSTEM, FEATURING A CYBER750 DIGITAL*
C* COMPUTER AND A CALCOMP PLOTTING FACILITY.  THE PROGRAM IS      *
C* WRITTEN IN FORTRAN IV EXTENDED VERSION L AND MAKES USE OF A    *
C* SIXTY BIT INTEGER WORD AND THE MEMORY MANIPULATION OPERATIONS *
C* AVAILABLE ON THAT SYSTEM.                                      *
C*****************************************************************
C
      PROGRAM DWBBF(INPUT,OUPUT,TAPE60=INPUT,TAPE61=OUTPUT,TAPE70)
      IMPLICIT INTEGER(A-Z)
      REAL DIST,ROTATE,DEPRES,ROTAT
C
C*****************************************************************
C*      THE PURPOSE OF THIS PROGRAM IS TO PRODUCE CRUDE IMAGES    *
C* OF HYPOTHETICAL BRYOZOAN COLONIES BASED UPON SEVERAL PARA-     *
C* METERS.  THESE ARE SUPPLIED, BY THE USER, AS MODIFICATIONS     *
C* TO THE DATA SET AT THE END OF THE PROGRAM.  THE PROGRAM RUNS   *
C* FOR THE DESIRED SET OF ITERATIONS AND PRODUCES, AS OUTPUT, A   *
C* A PLOT OF THREE SEPARATE VIEWS OF THE FORM GENERATED.  THIS    *
C* SIMULATED COLONY IS GENERATED IN A 50 X 50 MATRIX OF INTEGER   *
C* WORDS, USING EACH SUCCESSIVE BIT OF A WORD AS UNITS OF HEIGHT *
C* ABOVE THE SUBSTRATE.  THE FIRST BIT REPRESENTS A HEIGHT OF     *
C* ZERO UNITS AND THE SIXTIETH BIT A HEIGHT OF FIFTY NINE UNITS. *
C*     AN INITIAL POSITION (ANCESTRULA) IN THE FIRST BIT OF THE   *
C* WORD AT MATRIX POSITION (25,25) IS SET TO 1, SIGNIFYING THAT   *
C* IT IS OCCUPIED, AND THE 149,999 OTHERS ARE SET TO ZERO.  AS    *
C* THE FORM GROWS, ADDING TO THE INITIAL POSITION, THE VALUES     *
C* OF ADJACENT BITS ARE SELECTIVELY CHANGED FROM 0 TO 1.  IN      *
C* THIS WAY, THE SHAPE OF THE FORM CAN BE STORED AS IT LENGTHENS,*
C* THICKENS, BRANCHES, AND ANASTOMOSES, BECAUSE THE SPACES IT     *
C* OCCUPIES IN MEMORY ARE REPRESENTED BY A 1 AND THE SPACES WHICH*
C* SURROUND IT ARE REPRESENTED BY A 0.  THIS IMAGE IS PLOTTED.    *
C* IT IS ALSO COPIED ONTO A LOCAL FILE (TAPE 70), ASSIGNED A      *
C* PERMANENT FILE NAME AND CATALOGED AS A PERMANENT FILE.  AS     *
C* SUCH, IT NEEDS THE PROPER CONTROL CARDS TO ACCOMPLISH THIS     *
C* AFTER THE PROGRAM COMPLETES EXECUTION.  IN ADDITION, THE PARA-*
C* METERS IN THE DATA RECORD, VARIOUS DEBUGGING STATEMENTS, AND   *
C* AN OCTAL LISTING OF THE CENTRAL 20X20 SET OF WORDS IN THE      *
C* WORKSPACE ARE PRINTED AT THE END OF EACH STAGE OF THE RUN.     *
C*****************************************************************
C
C*****************************************************************
C*     IN THE FOLLOWING STATEMENT, "COLONY(50,50)" REPRESENTS THE*
C* WORKSPACE MATRIX.                                              *
C*****************************************************************
C
      COMMON /COMDAT/COLONY(50,50)
      COMMON /PLOTDAT/IBUF(513),DIST,ROTATE,DEPRES,ITERAT,ROTAT
      COMMON /SCALE/SCALER
      DATA MASK1/00000000000000000001B/
C
C*****************************************************************
C*      THE NEXT TWO STATEMENTS INITIATE THE PLOT.                *
C*****************************************************************
C
      CALL PLOTS(IBUF,513,0)
      CALL PSTART(DUMMY)
      WRITE (61,17)
 17   FORMAT(* IN MAIN1*)
C
C*****************************************************************
C*      THE FOLLOWING STATEMENT CALLS THE SUBROUTINE, "GROWER,"  *
C* WHICH GENERATES THE COLONY.                                    *
C*****************************************************************
C
      CALL GROWER(DUMMY)
      WRITE (61,18)
 18   FORMAT(* IN MAIN2*)
C
C*****************************************************************
C*      THE REMAINDER OF THE MAIN PROGRAM GENERATES THREE PLOTS   *
```

```
C* THAT REPRESENT DIFFERENT VIEWS OF THE FORM PRODUCED.          *
C*****************************************************************
C
      DO 188 EYE=1,3
        CALL FACTOR(1.0)
C
C******************************************************************
C*    THE FOLLOWING THREE STATEMENTS SET UP THE ORIGIN POINTS FOR *
C* EACH OF THE THREE VIEWS.                                       *
C******************************************************************
C
        IF(EYE.EQ.1)CALL PLOT(3.5,7.5,-3)
        IF(EYE.EQ.2)CALL PLOT(6.0,0.0,-3)
        IF(EYE.EQ.3)CALL PLOT(-6.0,-5.5,-3)
        WRITE (61,23)EYE
 23     FORMAT(* EYE=*,I1)
C
C******************************************************************
C*      THE FOLLOWING SET OF NESTED LOOPS PRODUCES PERSPECTIVE    *
C* DRAWINGS BY GOING THROUGH EACH BIT OF EACH WORD IN THE WORK-   *
C* SPACE AND COMPARING IT TO THE NEXT BIT BELOW IN THE SAME WORD  *
C* AND, IF THE TWO HAVE DIFFERENT VALUES, SUBROUTINE HORIZ IS     *
C* CALLED AND A HORIZONTAL LINE IS DRAWN (IN PERSPECTIVE,         *
C* ACCORDING TO THE ROTATION AND DEPRESSION DESIRED).  THEN THE   *
C* VALUE OF THE SAME BIT IS COMPARED TO THE VALUE OF THE BIT AT   *
C* THE SAME LEVEL IN THE ADJACENT WORD WITH THE SAME X-VALUE, BUT *
C* ONE HIGHER Y-VALUE.  IF THE BITS' TWO VALUES DIFFER, SUBROUTINE*
C* VERT IS CALLED AND A VERTICAL LINE IS DRAWN, IN PERSPECTIVE,   *
C* FOR THE POSITION TESTED.                                       *
C******************************************************************
C
      COFLAG=0
      X=1
  133 CONTINUE
        ENDFLAG=1
        DO 177 Z=2,60
          DO 166 Y=1,49
            SLICE=COLONY(X,Y)
            DICE=SHIFT(SLICE,1-Z).AND.MASK1
            YI=Y+1
            NUSLICE=COLONY(X,YI)
            NUDICE=SHIFT(NUSLICE,1-Z).AND.MASK1
            LODICE=SHIFT(SLICE,2-Z).AND.MASK1
            IF(DICE.EQ.LODICE)GO TO 144
              CALL HORIZ(X,Y,Z,EYE)
              ENDFLAG=0
              COFLAG=1
  144       CONTINUE
            IF(DICE.EQ.NUDICE)GO TO 155
              CALL VERT(X,Y,Z,EYE)
              ENDFLAG=0
              COFLAG=1
  155       CONTINUE
  166     CONTINUE
  177   CONTINUE
        X=X+1
C
C******************************************************************
C*     FOR EACH VALUE OF X, ALL THE BITS IN EACH WORD FOR EVERY   *
C* VALUE OF Y ARE SCANNED.  IT MAY OCCUR THAT, AFTER SCANNING ALL *
C* OCCUPIED PORTIONS OF THE WORKSPACE, SOME VALUES OF X MAY REMAIN*
C* THAT ARE SURE TO BE EMPTY.  IF THIS IS THE CASE, THE FOLLOWING *
C* STATEMENT ENDS FURTHER SCANNING.                               *
C******************************************************************
C
      IF(((COFLAG.EQ.0).OR.(ENDFLAG.EQ.0)).AND.(X.LT.50))GO TO 133
  188 CONTINUE
      CALL PLOT(12.0,0.0,999)
      END
C
C
C
```

```
      SUBROUTINE PSTART(DUMMY)
C
C****************************************************************
C*     THIS SUBROUTINE IS CALLED BY THE MAIN PROGRAM.  THE VARIOUS*
C* PARAMETERS NECESSARY FOR THE PLOTTING OF A SIMULATED BRYOZOAN  *
C* ARE INPUT IN THIS SUBROUTINE.  IN ADDITION, THE DESIRED NUMBER *
C* OF ITERATIONS, AN IMPORTANT PARAMETER IN THE SIMULATION ITSELF,*
C* IS ALSO INPUT HERE.  ITS VALUE IS THEN TRANSFERRED TO THE      *
C* SUBROUTINE THAT GROWS THE COLONY VIA A COMMON STATEMENT.       *
C****************************************************************
C
      IMPLICIT INTEGER(A-Z)
      REAL REPLY1,SCALER,DIST,ROTATE,DEPRES,FITERAT,ROTAT
      DIMENSION REPLY2(6)
      COMMON /COMDAT/COLONY(50,50)
      COMMON /PLOTDAT/IBUF(513),DIST,ROTATE,DEPRES,ITERAT,ROTAT
      COMMON /SCALE/SCALER
      DATA DIST/602./
      WRITE (61,20)
   20 FORMAT(* IN PSTART*)
      READ (60,8016)REPLY1
 8016 FORMAT(F4.2)
      WRITE (61,3001)REPLY1
 3001 FORMAT(* WHAT SCALING FACTOR WOULD YOU LIKE?---*,F4.2)
C
C****************************************************************
C$     THE UNITS USED BY THE PLOTTER ARE NEXT ALTERED FROM THE    *
C* DEFAULT OF 1 INCH TO THE PRODUCT OF 1 MILLIMETER TIMES THE     *
C* SCALING FACTOR REPRESENTED BY THE VALUE OF REPLY1.             *
C****************************************************************
C
      SCALER=0.0394*REPLY1
      CALL SYMBOL(8.0,1.0,.14,22HTHE SCALING FACTOR IS ,0.,22)
      CALL NUMBER(999.,999.,.14,REPLY1,0.,2)
      READ (60,3002)(REPLY2(I),I=1,6)
 3002 FORMAT(6A10)
      WRITE (61,3003)(REPLY2(I),I=1,6)
 3003 FORMAT(* TITLE OF THIS PLOT:*,/,* *,6A10)
      CALL SYMBOL(7.5,2.5,.14,REPLY2,0.,60)
      READ (60,8017)ITERAT
 8017 FORMAT(I2)
      WRITE (61,3004)ITERAT
 3004 FORMAT(* # OF ITERATIONS IN THIS RUN: *,I2)
      FITERAT=FLOAT(ITERAT)
      CALL SYMBOL(8.3,2.0,.10,28HTHE NUMBER OF ITERATIONS IS ,0.,28)
      CALL NUMBER(999.,999.,.10,FITERAT,0.,-1)
      CALL SYMBOL(7.8,1.8,.10,35HTHE NUMBER OF MM. TO THE VIEWER IS
     +,0.,35)
      CALL NUMBER(999.,999.,.10,DIST,0.,1)
      READ (60,8018)ROTATE
 8018 FORMAT(F10.5)
      WRITE (61,3005)
 3005 FORMAT(* THE OBJECT HAS BEEN ROTATED, IN THE CLOCKWISE DIRECTION,*
     +,/,* ABOUT THE Z-AXIS:*)
      WRITE (61,3006)ROTATE
 3006 FORMAT(* *,1X,F10.5,1X,*DEGREES.*)
      CALL SYMBOL(7.7,1.6,.10,10HTHERE ARE ,0.,10)
      CALL NUMBER(999.,999.,.10,ROTATE,0.,-1)
      CALL SYMBOL(999.,999.,.10,25H DEGREES OF LEFT ROTATION,0.,25)
      READ (60,8018)DEPRES
      WRITE (61,3007)DEPRES
 3007 FORMAT(* THE OBJECT HAS BEEN DEPRESSED, ABOUT THE X-AXIS,*
     +,/,* *,1X,F10.5,1X,*DEGREES.*)
      CALL SYMBOL(8.2,1.4,.10,DEPRES,0.,10)
      CALL NUMBER(999.,999.,.10,DEPRES,0.,-1)
      CALL SYMBOL(999.,999.,.10,22H DEGREES OF DEPRESSION,0.,22)
C
C****************************************************************
C*     THE VARIABLES "DEPRES" AND "ROTATE" ARE IN TERMS OF DEGREES*
C* HERE.  BUT IF THEY ARE TO BE USED WITH CERTAIN LIBRARY FUNC-   *
C* TIONS SUPPLIED BY THE COMPUTER SYSTEM, THEIR VALUES MUST BE    *
C* TRANSLATED TO RADIANS.  THE FOLLOWING STATEMENTS ACCOMPLISH    *
```

```
C* THIS.  BECAUSE THE DEGREE-VALUE OF ROTATE IS USED LATER IN THE *
C* PRODUCTION OF MULTIPLE PERSPECTIVE DRAWINGS, ITS VALUE IS       *
C* RETAINED AND THE TRANSLATION TO RADIANS IS ASSIGNED TO A NEW    *
C* VARIABLE "ROTAT."                                               *
C*****************************************************************
C
      DEPRES=DEPRES*0.01745
      ROTAT=ROTATE*0.01745
      RETURN
      END
C
C
C
      SUBROUTINE GROWER(DUMMY)
C
C*****************************************************************
C*     THIS SUBROUTINE IS CALLED BY THE MAIN PROGRAM.  THIS        *
C* SUBROUTINE READS IN THE VARIOUS GROWTH PARAMETERS, GENERATES    *
C* THE SIMULATED COLONY THROUGH THE DESIRED NUMBER OF ITERATIONS   *
C* AND RECORDS THE CONTENTS OF THE COLONY WORKSPACE ONTO A LOCAL   *
C* FILE (TAPE 70), WHICH IS CATALOGUED AS A PERMANENT FILE AT THE  *
C* END OF THE RUN.                                                 *
C*      THE SUBROUTINE CAN BE DIVIDED INTO SEVERAL PARTS, EACH     *
C* DEALING WITH A SPECIFIC ASPECT OF THE SIMULATION.               *
C*      FIRST THE VARIOUS PARAMETERS ARE READ IN AND IMMEDIATELY   *
C* ECHOED BACK AS OUTPUT.  THUS, THE INITIALIZATION PORTION IS     *
C* ESSENTIALLY SELF-EXPLANATORY.  SEE TABLE 1 (IN THE TEXT) FOR    *
C* INFORMATION ON ACCEPTABLE VALUE RANGES FOR SPECIFIC PARAMETERS.*
C*      SECOND IS A LARGE LOOP THAT EXECUTES ONCE FOR EACH         *
C* ITERATION OF THE SIMULATION.  EVERY ASPECT OF ERECT-GROWING,    *
C* DOUBLE-WALLED BRYOZOAN ASTOGENY THAT IS BEING SIMULATED IS      *
C* CONTAINED IN THIS LOOP.  THE LOOP CAN BE DIVIDED INTO FOUR      *
C* PARTS:  THE EXTENSION AND BIFURCATION OF BRANCH AXES, THE       *
C* MODIFICATION OF BRANCH GROWTH DIRECTIONS TO AVOID ANASTOMOSES,  *
C* THE GROWTH OF RECUMBENT PORTIONS OF THE COLONY, AND THE         *
C* THICKENING OF BRANCHES TO SIMULATE EXOZONAL GROWTH.             *
C*****************************************************************
C
      INTEGER COLONY,ITERAT,KAXIS,IHT,INCMNT,ZEROS,ISNK,
     +ITIME(32),ITBIFU,IRAND,NREPS,MASK1,GLOVER(50,50),
     +BUD,DICE(27),IDICE,XEXO
      REAL AXIS,GR,H,KAY,THETA,PHI,TIP,BASE(32,3),PHI1,THETA1,DISTIP,
     +ANGLE,TX,TY,TZ,XP,YP,ZP,X,Y,Z,XTERM,YTERM,ZTERM,PLAY,DIST,
     +CMAX,CRITCO,DSCONC(32),SCONC(32),DSCINI,RNF,RANDND,CHI,PSI,
     +RNDBIF,RANGE,XCOMP,YCOMP,RNUM,CRDIST,REP,BFDIST,AVMAG
     +RWIDTH(32)
      COMMON /COMDAT/COLONY(50,50)
      COMMON /PLOTDAT/IBUF(513),DIST,ROTATE,DEPRES,ITERAT,ROTAT
      COMMON /DIFFUS/CMAX,ISNK,CRITCO
      COMMON /REPS/REP(1000,3),AXIS(32,3),TIP(32,3)
C
C*****************************************************************
C*     THE FOLLOWING DATA STATEMENTS ASSIGN VALUES TO OCTAL        *
C* CONSTANTS THAT WILL BE USED TO INITIALIZE AND TEST (USING "IF" *
C* STATEMENTS) VARIOUS PORTIONS OF THE SIMULATION WORKSPACE.       *
C* TWENTY OCTAL DIGITS REPRESENT SIXTY BINARY BITS.  EACH X- AND   *
C* Y-VALUE IN THE WORKSPACE HAS A SIXTY-BIT BINARY WORD SIMULATING*
C* A SIXTY UNIT VERTICAL RANGE.  THUS, THE COLONY WORKSPACE, WHICH*
C* IS THE 50 BY 50 TYPE INTEGER ARRAY, COLONY(X,Y), HAS THE        *
C* DIMENSIONS 50 BY 50 BY 60.                                      *
C*****************************************************************
C
      DATA ZEROS/00000000000000000000B/,BUD/00000000000000000002B/
      DATA MASK1/00000000000000000001B/
      READ(60,1)GR
    1 FORMAT(F10.5)
      WRITE(61,2)GR
    2 FORMAT(* GROWTH RATE OF AXES: *,1X,F10.5)
C
C*****************************************************************
C*     THE FOLLOWING TWO PARAMETERS DETERMINE THE SHAPE OF THE     *
C* ENDOZONAL CROSS-SECTION OF A GROWING BRANCH AXIS.  IF THE       *
```

```
C* ENDOZONE IS TO HAVE A CIRCULAR CROSS-SECTION, H AND KAY SHOULD *
C* BE SET TO 1., IF ELLIPTICAL, ONE OF THE TWO SHOULD BE SET TO A *
C* VALUE BETWEEN O. AND 1.                                        *
C******************************************************************
C
      READ(60,1)H
      WRITE(61,3)H
    3 FORMAT(* ELLIPTIC RADII. H: *,F10.5)
      READ(60,1)KAY
      WRITE(61,4)KAY
    4 FORMAT(* K: *,F10.5)
      READ(60,1)CRITCO
      WRITE(61,7)CRITCO
    7 FORMAT(* ENDOZONE MORPHOGEN CRITCAL CONCENTRATION: *,F10.5)
      READ(60,1)CMAX
      WRITE(61,9)CMAX
    9 FORMAT(* MAXIMUM MORPHOGEN CONCENTRATION AT SOURCE: *,F10.5)
      READ(60,1)ANGLE
      WRITE(61,10)ANGLE
   10 FORMAT(* ANGLE OF BIFURCATION: *,F10.5)
      ANGLE=(ANGLE/57.3)/2
      READ(60,1)PLAY
      WRITE(61,11)PLAY
   11 FORMAT(* RANDOM PLAY IN BRANCH ANGLE: *,F10.5)
      PLAY=PLAY/57.3
      READ(60,12)ISNK
   12 FORMAT(I2)
      WRITE(61,73)ISNK
   73 FORMAT(* DISTANCE FROM SOURCE TO SINK: *,I1)
      READ(60,1)DSCINI
      WRITE(61,13)DSCINI
   13 FORMAT(* INITIAL GROWTH RATE FOR SOURCE STRENGTH: *,F10.5)
      READ(60,12)ITBIFU
      WRITE(61,14)ITBIFU
   14 FORMAT(* RECOVERY PERIOD AFTER A BIFURCATION: *,I1)
      READ(60,1)RNDBIF
      WRITE(61,15)RNDBIF
   15 FORMAT(* RANDOM VARIABILITY IN RECOVERY PERIOD: *,F10.5)
      READ(60,1)XCOMP
      WRITE(61,8001)XCOMP
 8001 FORMAT(* COMMON BUD GROWTH RATES. X COMPONENT: *,F10.5)
      READ(60,1)YCOMP
      WRITE(61,8002)YCOMP
 8002 FORMAT(* Y COMPONENT: *,10.5)
      READ(60,12)XEXO
      WRITE(61,8003)XEXO
 8003 FORMAT(* INVERSE FREQUENCY OF EXOZONE AUGMENTATION: *,I2)
      READ(60,1)CRDIST
      WRITE(61,8004)CRDIST
 8004 FORMAT(* CRITICAL DISTANCE FOR AUTO-AVOIDANCE: *,F10.5)
      READ(60,1)BFDIST
      WRITE(61,8005)BFDIST
 8005 FORMAT(* CRITICAL TIP DISTANCE FOR BRANCH INHIBITION: *,
     +F10.5)
      READ(60,1)AVMAG
      WRITE(61,8006)AVMAG
 8006 FORMAT(* AVOIDANCE MAGNITUDE: *,F10.5)
      DO 32 I=1,50
        DO 31 J=1,50
          COLONY(I,J)=ZEROS
   31   CONTINUE
   32 CONTINUE
      COLONY(25,25)=BUD
      AXIS(1,1)=0.0
      AXIS(1,2)=0.0
      AXIS(1,3)=GR
      BASE(1,1)=25.0
      BASE(1,2)=25.0
      BASE(1,3)=1.0
      TIP(1,1)=BASE(1,1)
      TIP(1,2)=BASE(1,2)
      TIP(1,3)=BASE(1,3)
```

```
      DSCONC(1)=DSCINI
      SCONC(1)=0.0
      RWIDTH(1)=0.0
      ITIME(1)=1
      KAXIS=1
      NREPS=0
C
C*********************************************************************
C*     THE FOLLOWING LOOP EXECUTES ONCE FOR EACH ITERATION OF THE *
C* SIMULATION.  IT CAN BE DIVIDED INTO FOUR PARTS.  THE FIRST IS A*
C* LOOP THAT: DETERMINES THE WIDTH, GROWTH DIRECTION, AND LENGTH  *
C* OF ADDITIONS TO EACH GROWING TIP, FINDS THEIR POSITIONS IN THE *
C* WORKSPACE "COLONY(X,Y)," ALTERS THE VALUES OF BITS CORRES-     *
C* ING TO THOSE POSITIONS IN THE WORKSPACE TO INDICATE THAT THEY  *
C* ARE FILLED, ASSIGNS VALUES TO VARIABLES THAT WILL REPRESENT THE*
C* POSITIONS OF THESE NEWLY GROWN COLONY PARTS IN THE EXECUTION OF*
C* THE AVOIDANCE MECHANISM, DECIDES WHETHER OR NOT ANY OF THE     *
C* EXISTING BRANCH AXES IS READY TO BIFURCATE, AND IF SO,         *
C* INITIATES THE NEW BRANCH AXIS.                                 *
C*     THE SECOND PART IS A STATEMENT THAT CALLS THE SUBROUTINE   *
C* "AVOID," WHICH ALTERS THE GROWTH DIRECTION OF EACH AXIS        *
C* (INCLUDING NEWLY INITIATED ONES) IN ORDER TO INHIBIT THE       *
C* TENDENCY OF BRANCHES TO GROW INTO ONE ANOTHER.                 *
C*     THE THIRD PART EXTENDS THE RECUMBENT BASAL PORTIONS OF THE *
C* SIMULATED COLONY AND FILLS IN THE CORRESPONDING PORTIONS OF THE*
C* WORKSPACE.                                                     *
C*     THE FOURTH PORTION ONLY OPERATES IN A FRACTION OF THE TOTAL*
C* NUMBER OF ITERATIONS.  IT SIMULATES THE SLOW GROWING EXOZONAL  *
C* PORTIONS OF THE COLONY, WHICH IN ERECT FORMS, SERVES TO THICKEN*
C* OLDER MORE MATURE PARTS OF THE COLONY.  A SECOND WORKSPACE,    *
C* "GLOVER(X,Y)," IS INITIATED, THE ORIGINAL WORKSPACE IS SCANNED,*
C* AND THE SET OF ADJACENT PERIPHERAL POINTS IS FILLED IN         *
C* GLOVER(X,Y).  EXOZONAL GROWTH IS THEN SIMULATED BY ADDING THE  *
C* CONTENTS OF GLOVER(X,Y) TO COLONY(X,Y) USING THE ".OR."        *
C* OPERATION.                                                     *
C*********************************************************************
C
      DO 215 NUM=1,ITERAT
        KAX=KAXIS
C
C*********************************************************************
C*     THE FOLLOWING LOOP EXECUTES ONCE FOR EACH BRANCH AXIS      *
C* EXISTING AT THE BEGINNING OF THE CURRENT ITERATION.            *
C*********************************************************************
C
        DO 234 N=1,KAX
C
C*********************************************************************
C*     THE FOLLOWING STATEMENT CALLS THE SUBROUTINE "WIDTH."  THE *
C* VALUES FOR ENDOZONAL WIDTH (RWIDTH), CONCENTRATION OF ENDOZONE *
C* PRODUCING MORPHOGEN (SCONC) AND THE RATE OF CHANGE OF THIS     *
C* SOURCE CONCENTRATION THROUGH TIME (DSCONC), FOR EACH BRANCH    *
C* AXIS UNDER CONSIDERATION, ARE TRANSFERRED THROUGH THE CALL     *
C* STATEMENT.  THE VARIOUS CONSTANT PARAMETERS NEEDED FOR SUB-    *
C* ROUTINE WIDTH ARE TRANSFERRED VIA COMMON STATEMENTS.  IF THE   *
C* ENDOZONE WIDTH OR SOURCE CONCENTRATION IS AT ZERO, ALL GROWTH  *
C* PROCESSES SIMULATED FOR THE PARTICULAR BRANCH AXIS THIS        *
C* ITERATION (EXCEPT FOR EXOZONAL GROWTH) ARE SKIPPED.            *
C*********************************************************************
C
          CALL WIDTH(DSCONC(N),RWIDTH(N),SCONC(N))
          IF(SCONC(N).LE.0.)GO TO 234
          IF(RWIDTH(N).LE.0.)GO TO 234
C
C********************************************************************
C*     THE FOLLOWING FOURTEEN LINES SERVE TO ADD THE RANDOM      *
C* COMPONENT TO AN INDIVIDUAL BRANCH'S GROWTH DIRECTION.         *
C********************************************************************
C
          PHI=ACOS(AXIS(N,3)/GR)
          IF(PHI.EQ.0.)PHI=0.00001
          THETA=ACOS(AXIS(N,1)/(GR*SIN(PHI)))
```

```
      IF(AXIS(N,2).LT.O.)THETA=-THETA
      RNF=RANF(X)
      RANDND=.62666*ALOG((1.+RNF)/(1.-RNF))
      PHI1=(PLAY/3.)*RANDND
      THETA=RANF(X)*6.2832
      AXIS(N,1)=GR*COS(PHI1)*COS(THETA)*SIN(PHI)+GR*SIN(PHI1)*
     +(SIN(THETA1)*SIN(THETA)-COS(THETA1)*COS(THETA)*COS(PHI))
      AXIS(N,2)=GR*COS(PHI1)*SIN(THETA)*SIN(PHI)+GR*SIN(PHI1)*
     +(-SIN(THETA1)*COS(THETA)-COS(THETA1)*SIN(THETA)*COS(PHI))
      AXIS(N,3)=GR*COS(PHI1)*COS(PHI)+GR*SIN(PHI1)*
     +COS(THETA1)*SIN(PHI)
C
C***********************************************************************
C*     THE FOLLOWING SET OF NESTED LOOPS SERVES TO RECORD THE          *
C* BRANCH'S ENDOZONAL GROWTH INTO THE COLONY WORKSPACE.  EACH          *
C* POINT IN THE WORKSPACE IS INDIVIDUALLY TESTED FOR INCLUSION.        *
C***********************************************************************
C
      DO 653 I=1,50
        DO 652 J=1,50
          DO 651 L=1,50
C
C***********************************************************************
C*     THE FOLLOWING ASSIGNMENTS ARE MADE WITH THE HOPE OF             *
C* RENDERING THE CALCULATIONS THAT FOLLOW LESS CLUTTERED.              *
C***********************************************************************
C
            X=FLOAT(I)
            Y=FLOAT(J)
            Z=FLOAT(K)
            TX=TIP(N,1)
            TY=TIP(N,2)
            TZ=TIP(N,3)
            XP=BASE(N,1)
            YP=BASE(N,2)
            ZP=BASE(N,3)
            A=AXIS(N,1)
            B=AXIS(N,2)
            C=AXIS(N,3)
C
C***********************************************************************
C*     THE NEWLY GROWN PART OF EACH BRANCH IS SIMULATED AS A           *
C* SEGMENT OF A CYLINDER ADDED ON TO THE PREVIOUS BRANCH TIP.          *
C* THE POINTS, CORRESPONDING TO THIS CYLINDER, WHICH WILL BE           *
C* ADDED TO THE COLONY IMAGE IN THE WORKSPACE, ARE BOUNDED BY THE*
C* CYLINDER, ORIENTED IN THREE-SPACE, A PAIR OF PARALLEL PLAINS  *
C* WHICH ARE NORMAL TO THE DIRECTRIX OF THE CYLINDER (THE GROWTH *
C* DIRECTION) AND COINCIDENT WITH THE OLD AND NEW POSITIONS OF   *
C* THE BRANCH TIP.  THE TWO STATEMENTS FOLLOWING WILL ELIMINATE  *
C* FROM CONSIDERATION ALL POINTS THAT DO NOT LIE BETWEEN THESE   *
C* PLANES FOR ANY GIVEN BRANCH AXIS.                             *
C***********************************************************************
C
            IF((A*(X-TX)+B*(Y-TY)+C*(Z-TZ)).LT.O.)GO TO 651
            IF((A*(X-(TX+A))+B*(Y-(TY+B))+C*(Z-(TZ+C))).GT.
     +O.)GO TO 651
C
C***********************************************************************
C*     THE FOLLOWING SET OF TRANSFORMATIONS AND IF-STATEMENT WILL*
C* ELIMINATE POINTS NOT FOUND WITHIN THE CYLINDER FROM           *
C* CONSIDERATON FOR INCLUSION IN THE WORKSPACE.                  *
C***********************************************************************
C
              PSI=ASIN(AXIS(N,1)/GR)
              CHI=ACOS(AXIS(N,3)/(COS(PSI)*GR))
              IF(AXIS(N,2).GT.O.O)CHI=-CHI
              XTERM=(X-TX)*COS(PSI)+(Y-TY)*SIN(CHI)*SIN(PSI)
     +-(Z-TZ)*COS(CHI)*SIN(PSI)
              YTERM=(Y-TY)*COS(CHI)+(Z-TZ)*SIN(CHI)
              ZTERM=(X-TX)*SIN(PSI)-(Y-TY)*SIN(CHI)*COS(CHI)
     ++(Z-TZ)*COS(CHI)*COS(PSI)
              IF(ZTERM.EQ.O.)ZTERM=0.00001
```

```
                    IF((XTERM**2/H**2+YTERM**2/KAY**2).GT.RWIDTH(N))
     +GO TO 651
C
C****************************************************************
C*     IF A POINT(I,J,L) IS FOUND TO BE INCLUDE IN THE NEWLY      *
C* GROWN BRANCH SEGMENT, IT IS ADDED TO THE IMAGE IN THE          *
C* WORKSPACE BY THE FOLLOWING ALGORITHM.  THE L-COORDINATE IS THE*
C* HEIGHT (CORRESPONDING TO Z-VALUES IN THE WORKSPACE).  AN       *
C* INTEGER WORD IS INITIATED, WHICH HAS THE FIRST FIFTY-NINE BITS*
C* SET TO ZERO AND THE SIXTIETH BIT SET TO ONE, REPRESENTING AN  *
C* ERECT COLUMN SIXTY BITS HIGH WITH THE BOTTOM-MOST UNIT FILLED *
C* AND ALL ABOVE IT UNOCCUPIED.  THE *SHIFT* OPERATION, AVAILABLE*
C* ON THE MICHIGAN STATE UNIVERSITY COMPUTER SYSTEM, IS USED TO  *
C* MOVE THE FILLED BIT TO THE LEFT IN THE INTEGER WORD, FROM THE *
C* LAST (ZERO HEIGHT OR SIXTIETH) POSITION TO A POSITION         *
C* CORRESPONDING TO THE HEIGHT OF THE L-COORDINATE.  THE *.OR.*  *
C* OPERATION THEN ADDS THIS FILLED BIT TO THE WORD IN THE        *
C* WORKESPACE HOLDING ALL THE POINTS WITH X- AND Y-COORDINATES   *
C* CORRESPONDING TO THE CURRENT VALUES OF J AND K.               *
C****************************************************************
C
                      IHT=L
                      IMASK=MASK(1)
                      INCMNT=SHIFT(IMASK,IHT)
                      COLONY(I,J)=COLONY(I,J).OR.INCMNT
  651           CONTINUE
  652         CONTINUE
  653       CONTINUE
C
C****************************************************************
C*     THE BRANCH TIP IS EXTENDED.                                *
C****************************************************************
C
            TIP(N,1)=TIP(N,1)+AXIS(N,1)
            TIP(N,2)=TIP(N,2)+AXIS(N,2)
            TIP(N,3)=TIP(N,3)+AXIS(N,3)
C
C****************************************************************
C*     FOR THE PURPOSE OF THE AVOIDANCE SIMULATION, REPRESENTA-   *
C* TIVE POINT-LOCATIONS OF EACH PORTION OF THE COLONY ARE KEPT.   *
C* NOTICE THAT IF MORE THAN A THOUSAND REPRESENTATIVE POINT-      *
C* LOCALITIES ARE RECORDED, THE SIMULATION IS TERMINATED AND THE *
C* PARTIAL RESULTS ARE RECORDED AND RETURNED TO THE MAIN PROGRAM.*
C****************************************************************
C
            NREPS=NREPS+1
            IF(NREPS.EQ.1000)WRITE(61,1000)
 1000       FORMAT(* NUMBER OF REPS EXCEEDED.*)
            IF(NREPS.EQ.1000)GO TO 555
            REP(NREPS,1)=TIP(N,1)
            REP(NREPS,2)=TIP(N,2)
            REP(NREPS,3)=TIP(N,3)
C
C****************************************************************
C*     THE REMAINDER OF THIS LOOP TESTS THE BRANCH AXIS TO SEE    *
C* WHETHER OR NOT A BIFURCATION IS TO OCCUR.  IF THE TIME SINCE   *
C* THE PREVIOUS BIFURCATION, GIVEN A RANDOM COMPONENT, IS         *
C* INSUFFICIENT OR IF THE SOURCE CONCENTRATION OF THE ENDOZONE-   *
C* PRODUCING MORPHOGEN IS BELOW A CRITICAL LEVEL (SIMULATING      *
C* EARLY ASTOGENY) OR IF BIFURCATION IS BEING INHIBITED DUE TO    *
C* PROXIMITY OF OTHER BRANCH TIPS, THE BRANCH BIFURCATION WILL    *
C* NOT TAKE PLACE.  HOWEVER, IF THE DECISION IS MADE TO           *
C* BIFURCATE, THE AXIS COUNTER IS INCREASED BY ONE AND A NEW      *
C* BRANCH AXIS IS INITIALIZED, THE GROWTH DIRECTION OF THE        *
C* PARENT IS DEFLECTED TO THE SIDE TO SIMULATE DICHOTOMOUS        *
C* BRANCHING, AND THE BIFURCATION RECOVERY TIMERS ARE (RE)SET TO *
C* THE CURRENT ITERATION.  IF THE NUMBER OF BRANCH AXES AT THIS  *
C* TIME EXCEEDS THIRTY-TWO, THE SIMULATION IS TERMINATED AND THE *
C* PARTIAL RESULTS ARE STORED AND RETURNED TO THE MAIN PROGRAM.  *
C****************************************************************
C
            RANGE=SQRT(-2*ALOG(RANF(X)))*SIN(6.2832*RANF(X))*(RNDBIF/3.)
```

```
      IRAND=IFIX(RANGE+.5)
      IF(RANGE.LT.O.)IRAND=IFIX(RANGE-.5)
      IF((NUM-ITIME(N)+IRAND.LT.ITBIFU).OR.(SCONC(N).LT.CMAX))
     +GO TO 234
        DO 90 KA=1,KAXIS
          IF(N.EQ.KA)GO TO 90
            DISTIP=SQRT((TIP(KA,1)-TIP(N,1))**2.+(TIP(KA,2)-
     +TIP(N,2))**2.+(TIP(KA,3)-TIP(N,3))**2.)
            IF(DISTIP.LE.BFDIST)GO TO 234
 90     CONTINUE
        KAXIS=KAXIS+1
        IF(KAXIS.LT.33)GO TO 888
          WRITE(61,887)NUM
887       FORMAT(* AXIS LIMIT, ITERATION *,I3)
          GO TO 555
888     CONTINUE
        AXIS(N,1)=SIN(PSI+ANGLE)*GR
        AXIS(N,2)=-SIN(CHI)*COS(PSI+ANGLE)*GR
        AXIS(N,3)=COS(CHI)*COS(PSI+ANGLE)*GR
        BASE(N,1)=TIP(N,1)
        BASE(N,2)=TIP(N,2)
        BASE(N,3)=TIP(N,3)
        ITIME(N)=NUM
        AXIS(KAXIS,1)=SIN(PSI-ANGLE)*GR
        AXIS(KAXIS,2)=-SIN(CHI)*COS(PSI-ANGLE)*GR
        AXIS(KAXIS,3)=COS(CHI)*COS(PSI-ANGLE)*GR
        BASE(KAXIS,1)=TIP(N,1)
        BASE(KAXIS,2)=TIP(N,2)
        BASE(KAXIS,3)=TIP(N,3)
        TIP(KAXIS,1)=BASE(KAXIS,1)
        TIP(KAXIS,2)=BASE(KAXIS,2)
        TIP(KAXIS,3)=BASE(KAXIS,3)
        DSCONC(KAXIS)=DSCONC(N)
        SCONC(KAXIS)=SCONC(N)
        RWIDTH(KAXIS)=RWIDTH(N)
        ITIME(KAXIS)=NUM
 234  CONTINUE
C
C*****************************************************************
C*     THE FOLLOWING STATEMENT CALLS THE AVOIDANCE MECHANISM     *
C* SUBROUTINE, WHICH WILL READJUST THE GROWTH VECTORS OF EACH    *
C* AXIS EXISTING DURING THE CURRENT ITERATION.  THE VARIABLES    *
C* TRANSFERRED ARE THE AXIS AND POINT-LOCALITY REPRESENTATIVE    *
C* COUNTERS ALONG WITH THE PARAMETERS FOR CRITICAL AVOIDANCE     *
C* DISTANCE AND THE MAGNITUDE OF AVOIDANCE.  OTHER VARIABLES,    *
C* THE LOCATIONS OF REPRESENTATIVE POINT-LOCALITIES, AXIAL GROWTH*
C* VECTORS, AND BRANCH TIP COORDINATES, BEING COMPOUND VARIABLE  *
C* ARRAYS, ARE TRANSFERRED BETWEEN SUBROUTINES USING A COMMON    *
C* STATEMENTS.                                                   *
C*****************************************************************
C
      CALL AVOID(NREPS,KAXIS,CRDIST,AVMAG)
 235  CONTINUE
C
C*****************************************************************
C*     THE FOLLOWING STATEMENTS ALLOW FOR THE SIMULATION OF THE  *
C* GROWTH OF RECUMBENT PORTIONS.  THE GROWTH RATE OF THIS BASAL  *
C* ENCRUSTING PORTION OF THE COLONY IS SIMPLY MODELLED AS RADIAL *
C* GROWTH, DIRECTLY RELATED TO ELAPSED TIME.  DIFFERENT GROWTH   *
C* RATES IN THE X- AND Y-DIRECTIONS CAN BE ACCOMODATED BY USING  *
C* DIFFERENT VALUES FOR THE PARAMETERS "XCOMP" AND "YCOMP."      *
C*****************************************************************
C
      RNUM=FLOAT(NUM)
      DO 333 M=1,49
        DO 332 N=1,49
          IF((COLONY(M,N).AND.BUD).NE.ZEROS)GO TO 332
            IF(((COLONY(M-1,N-1).AND.BUD).EQ.ZEROS).AND.
     +((COLONY(M-1,N).AND.BUD).EQ.ZEROS).AND.((COLONY(M-1,N+1)
     +.AND.BUD).EQ.ZEROS).AND.((COLONY(M,N-1).AND.BUD).EQ.ZEROS)
     +.AND.((COLONY(M,N+1).AND.BUD).EQ.ZEROS).AND.((COLONY(M+1,
     +N-1).AND.BUD.).EQ.ZEROS).AND.((COLONY(M+1,N+1).AND.BUD).EQ.
```

```
     +ZEROS).AND.((COLONY(M+1,N+1).AND.BUD).EQ.ZEROS))GO TO 332
                X=FLOAT(M)
                Y=FLOAT(N)
                IF((X-25.)**2./(XCOMP*RNUM)**2.+(Y-25.)**2./
     +(YCOMP*RNUM)**2..LE.1.)COLONY(M,N)=COLONY(M,N).OR.BUD
  332       CONTINUE
  333     CONTINUE
C
C*****************************************************************
C*     THE REMAINING PORTION OF THE GROWTH SIMULATION IS THE     *
C* SIMULATION OF EXOZONAL GROWTH.  BECAUSE THE EXOZONE GROWS MUCH*
C* MORE SLOWLY THAN THE ENDOZONE, IT CANNOT BE SIMULATED DURING  *
C* EVERY ITERATION.  THIS IS ALSO DUE TO THE LIMITED RESOLUTION  *
C* CAPACITY OF THE WORKSPACE.  THE PARAMETER "XEXO" DETERMINES   *
C* HOW OFTEN THE CODE THAT FOLLOWS WILL BE ACCESSED.             *
C*****************************************************************
C
        IF(NUM.GT.(NUM/XEXO)*XEXO)GO TO 215
C
C*****************************************************************
C*     THE EXOZONE SIMULATION BEGINS BY INITIALIZING A SECOND    *
C* WORKSPACE,"GLOVER(X,Y)," WITH OCTAL (AND THEREFORE BINARY)    *
C* ZEROS.  THIS EMPTY WORKSPACE WILL BE USED TO HOLD,            *
C* TEMPORARILY, THE LOCATIONS OF THE SET OF POINTS ADJACENT TO   *
C* THE POINTS CURRENTLY FILLED IN THE WORKSPACE, COLONY(X,Y).    *
C*****************************************************************
C
          DO 335 IG=1,50
            DO 334 JG=1,50
              GLOVER(IG,JG)=ZEROS
  334       CONTINUE
  335     CONTINUE
C
C*****************************************************************
C*     IN THE FOLLOWING SET OF NESTED LOOPS, THE EXOZONAL GROWTH *
C* FOR THE CURRENT ITERATION IS GENERATED AND THEN ADDED TO THE  *
C* WORKSPACE "COLONY(X,Y)."  EACH POINT IS TESTED FOR INCLUSION  *
C* IN THE EXOZONAL GROWTH FOR THE CURRENT ITERATION.  FIRST THE  *
C* POINT MUST BE FOUND TO BE UNOCCUPIED.  THEN EACH OF THE       *
C* TWENTY-SIX ADJACENT POINTS IS TESTED TO SEE IF AT LEAST ONE IS*
C* OCCUPIED.  IF AT LEAST ONE OF THE ADJACENT POINTS IS OCCUPIED,*
C* A SINGLE BIT IS SET TO ONE (FILLED) IN THE TEMPORARY          *
C* WOKSPACE, GLOVER(X,Y), AT THE COORDINATES CORRESPONDING TO THE*
C* POSITION OF THE POINT UNDER SCRUTINY.  AFTER EVERY POINT IN   *
C* THE WORKSPACE HAS BEEN SO TESTED AND THE APPROPRIATE ONES     *
C* FILLED IN THE WORKSPACE, THE IMAGE IN COLONY(X,Y) IS REPLACED *
C* BY THE UNION OF THE SETS OF POINTS IN COLONY(X,Y) AND         *
C* GLOVER(X,Y).                                                  *
C*****************************************************************
C
          DO 444 I=2,49
            DO 443 J=2,49
              DO 442 K=2,59
                IDICE=SHIFT(COLONY(I,J),1-K).AND.MASK1
                IF(IDICE.NE.ZEROS)GO TO 442
                  IM=I-1
                  JM=J-1
                  IP=I+1
                  IM=J+1
                  KM=K-2
                  KOUNT=0
                  DO 441 II=IM,IP
                    DO 440 JJ=JM,JP
                      DO 439 KK=KM,K
                        KOUNT=KOUNT+1
                        DICE(KOUNT)=SHIFT(COLONY(II,JJ),-KK).AND.
     +MASK1
  439                 CONTINUE
  440               CONTINUE
  441             CONTINUE
                  KTR=0
   16             CONTINUE
```

```
                  KTR=KTR+1
                  IF(DICE(KTR).EQ.MASK1)GLOVER(I,J)=GLOVER(I,J)
     +.OR.SHIFT(MASK(1),K)
                  IF(DICE(KTR).EQ.MASK1)GO TO 442
                IF(KTR.LT.27)GO TO 16
  442         CONTINUE
  443       CONTINUE
  444     CONTINUE
          DO 556 I=1,50
            DO 554 J=1,50
              COLONY(I,J)=COLONY(I,J).OR.GLOVER(I,J)
  554       CONTINUE
  556     CONTNUE
  215 CONTINUE
  555 CONTINUE
C
C*****************************************************************
C*     AFTER COMPLETING THE SIMULATION, THE VALUES OF THE CENTRAL*
C* TWENTY X-COORDINATES AND Y-COORDINATES OF THE WORKSPACE ARE   *
C* PRINTED IN OCTAL FORMAT.  THESE ARE FOLLOWED BY A STATEMENT OF*
C* THE TOTAL NUMBER OF AXES GENERATED DURING THE SIMULATION.     *
C*****************************************************************
C
      WRITE(61,666)((COLONY(I,J),I=16,20),J=16,35)
  666 FORMAT(1H ,O20,1X,O20,1X,O20,1X,O20,1X,O20)
      WRITE(61,666)((COLONY(I,J),I=21,25),J=16,35)
      WRITE(61,666)((COLONY(I,J),I=26,30),J=16,35)
      WRITE(61,666)((COLONY(I,J),I=31,35),J=16,35)
      WRITE(61,776)KAXIS
  776 FORMAT(* THE ORGINAL AXIS HAS DIVIDED INTO *,I2,* BANCHES.*)
C
C*****************************************************************
C*     THE FOLLOWING STATEMENT CAUSES THE X-,Y-, AND Z-VALUES FOR*
C* THE GROWTH VECTORS, BRANCH SEGMENT BASES, AND BRANCH TIPS FOR *
C* EACH BRANCH AXIS GENERATED TO BE PRINTED FOR ANALYSIS.        *
C*****************************************************************
C
      WRITE(61,775)((AXIS(I,J),J=1,3),(BASE(I,J),J=1,3),(TIP(I,J),J=3)
     +,I=1,KAXIS)
  775 FORMAT(1H ,9F10.4)
C
C*****************************************************************
C*     THE TOTAL CONTENTS OF THE SIMULATION WORKSPACE ARE COPIED *
C* ONTO TAPE70 IN OCTAL FORMAT, WHICH WILL BE CATALOGED AS A     *
C* PERMANENT FILE AT THE END OF THE RUN.                         *
C*****************************************************************
C
      DO 7766 I=1,50
        WRITE(70,7765)(COLONY(I,J),J=1,50)
 7765   FORMAT(50O20)
 7766 CONTINUE
      RETURN
      END
C
C
C
      SUBROUTINE WIDTH(DSCONC,RWIDTH,SCONC)
C
C*****************************************************************
C*     CALLED BY SUBROUTINE GROWER, THE PURPOSE OF THIS          *
C* SUBROUTINE IS TO SIMULATE THE STEADY-STATE DIFFUSION OF AN    *
C* ENDOZONE-INDUCING MORPHOGEN FROM A POINT-SOURCE AT THE BRANCH *
C* TIP TO A SINK THAT IS A PREDETERMINED DISTANCE AWAY.  THE     *
C* SUBROUTINE RETURNS VALUES FOR THE RATE OF CHANGE OF THE LEVEL *
C* OF ENDOZONE MORPHOGEN AT ITS SOURCE, THE COMPUTED WIDTH OF THE*
C* ENDOZONE, AND THE COMPUTED CONCENTRATION OF MORPHOGEN AT THE  *
C* SOURCE FOR THE BRANCH AXIS UNDER CONSIDERATION.  WHEN THE     *
C* SOURCE CONCENTRATION OF THE MORPHOGEN REACHES A CERTAIN       *
C* MAXIMUM VALUE, THE RATE OF INCREASE IS SET TO ZERO.  THE      *
C* COMPUTED WIDTH OF THE ENDOZONE IS DEPENDENT ON THE            *
C* PREDETERMINED DISTANCE FROM SOURCE TO SINK, THE CRITCAL       *
C* CONCENTRATION OF MORPHOGEN NEEDED TO INDUCE ENDOZONE, AND THE *
```

```
C* COMPUTED CONCENTRATION AT THE SOURCE.                              *
C*********************************************************************
C
      REAL DSCONC,SCONC,CMAX,CRITCO,RSNK,RWIDTH
      INTEGER ISNK
      COMMON/DIFFUS/CMAX,ISNK,CRITCO
      IF(SCONC.GE.CMAX)DSCONC=0.
      SCONC=SCONC+DSCONC
      RSNK=FLOAT(ISNK)
      RWIDTH=RSNK*(1.-(CRITCO/SCONC))
      RETURN
      END
C
C
C
      SUBROUTINE AVOID(NREPS,KAXIS,CRDIST,AVMAG)
C
C*********************************************************************
C*     CALLED BY SUBROUTINE GROWER, THE PURPOSE OF THIS               *
C* SUBROUTINE IS TO MODIFY THE GROWTH DIRECTIONS OF EACH BRANCH       *
C* AXIS (THAT EXISTS IN THE ITERATION IN WHICH IT IS CALLED) IN       *
C* ORDER TO DECREASE THE POSSIBILITY OF BRANCHES GROWING INTO ONE*
C* ANOTHER'S PATH.  THE GROWTH DIRECTION IS SEEN AS A VECTOR AND *
C* THE GROWTH RATE AS ITS MAGNITUDE.  THE EFFECT OF THE AVOIDANCE*
C* MECHANISM IS THAT THE GROWING TIP IS ABLE TO SENSE THE             *
C* PROXIMITY AND COMPOSITE DIRECTION OF OTHER PARTS OF THE COLONY*
C* AND CAN USE THIS INFORMATION TO MODIFY THE DIRECTION OF ITS  *
C* GROWTH AND THEREBY AVOID OVERCROWDING.  EACH PORTION OF THE        *
C* COLONY HAS A REPESENTATIVE POINT LOCALITY IN STORAGE.              *
C*********************************************************************
C
      INTEGER NREPS,KAXIS
      REAL AXIS,REP,NORM,DIST,TIP,MAGTUD
      COMMON/REPS/REP(1000,3),AXIS(32,3),TIP(32,3)
      DO 201 L=1,KAXIS
        MAGTUD=SQRT(AXIS(L,1)**2.+AXIS(L,2)**2.+AXIS(L,3)**2.)
C
C*********************************************************************
C*     IF ANY PART OF THE COLONY IS WITHIN A CERTAIN CRITICAL         *
C* DISTANCE FROM THE BRANCH TIP IN QUESTION, IT IS CONSIDERED IN *
C* THE AVOIDANCE FIELD.  THE FOLLOWING EXAMINES EACH                  *
C* REPRESENTATIVE POINT-LOCALITY.  THE EFFECT OF THE MODIFICATION*
C* OF EACH COLONY PART ON THE COMPONENTS OF A BRANCH'S GROWTH         *
C* VECTOR IS DEPENDENT UPON ITS DIRECTION, DISTANCE, AND THE          *
C* SENSITIVITY OF THE BRANCH TIP AS SEEN IN THE VIGOR (OR             *
C* MAGNITUDE) OF ITS AVOIDANCE RESPONSE.  THE EFFECT OF EACH          *
C* ELIGIBLE COLONY PART IS ADDED TO THE VECTOR COMPONENTS.            *
C*     THE VARIABLE "AVMAG," READ INTO AND TRANSFERED HERE FROM       *
C* SUBROUTINE "GROWER," SHOULD BE EXPLAINED FULLY.  ESSENTIALLY       *
C* IT IS THE MAGNITUDE OF THE AVOIDANCE REACTION.  THE LOWER ITS *
C* VALUE, THE MORE THE MODIFIED GROWTH DIRECTION IS DEPENDENT ON *
C* THE PREVIOUS GROWTH DIRECTION.  THE GREATER ITS VALUE, THE         *
C* MORE THE MODIFIED GROWTH DIRECTION IS DEPENDENT ON THE             *
C* PROXIMITY AND LOCATIONS OF NEIGHBORING COLONY PARTS.  A VALUE *
C* OF 1.0 WILL CAUSE A NEIGHBORING REPRESENTATIVE LOCALITY, ONE  *
C* UNIT DISTANT TO HAVE THE SAME INTENSITY OF EFFECT AS WOULD THE*
C* CURRENT GROWTH VECTOR IF "GR" ALSO CONTAINED A VALUE OF 1.0.  *
C* IF THE ENDOZONE EXTENSION RATE ("GR") WERE 6.0, THEN "AVMAG"  *
C* WOULD HAVE TO CONTAIN THE SAME VALUE IF THE EFFECT OF A ONE-  *
C* UNIT DISTANT NEIGHBOR WERE TO EQUAL THE GROWTH VECTOR'S.      *
C*********************************************************************
C
        DO 190 LA=1,NREPS
          DIST=SQRT((REP(LA,1)-TIP(L,1))**2.+(REP(LA,2)-TIP(L,2)
     +)**2.+(REP(LA,3)-TIP(L,3))**2.)
          IF((DIST.GT.CRDIST).OR.(DIST.EQ.0.))GO TO 190
            AXIS(L,1)=AXIS(L,1)+AVMAG*(TIP(L,1)-REP(LA,1))/DIST**2.
            AXIS(L,2)=AXIS(L,2)+AVMAG*(TIP(L,2)-REP(LA,2))/DIST**2.
            AXIS(L,3)=AXIS(L,3)+AVMAG*(TIP(1,3)-REP(LA,3))/DIST**2.
  190   CONTINUE
C
C*********************************************************************
```

```
C*     THE NEW VECTOR DIRECTION IS CONVERTED TO A UNIT VECTOR AND*
C* THEN GIVEN THE ORIGINAL MAGNITUDE OF THE GROWTH VECTOR.       *
C****************************************************************
C
        NORM=SQRT(AXIS(L,1)**2.+AXIS(L,2)**2.+AXIS(L,3)**2.)
        AXIS(L,1)=(AXIS(L,1)/NORM)*MAGTUD
        AXIS(L,2)=(AXIS(L,2)/NORM)*MAGTUD
        AXIS(L,3)=(AXIS(L,3)/NORM)*MAGTUD
  201 CONTINUE
      RETURN
      END
C
C
C
      SUBROUTINE HORIZ(X,Y,Z,EYE)
C
C****************************************************************
C*     CALLED BY THE MAIN PROGRAM, THIS SUBROUTINE TAKES A SET OF*
C* COORDINATES, DEEMED BY THE MAIN PROGRAM TO REPRESENT A        *
C* HORIZIONTAL BOUNDARY BETWEEN AN OCCUPIED SPACE AND AN EMPTY   *
C* SPACE IN THE COMPLETED COLONY WORKSPACE, AND DRAWS A          *
C* REPRESENTATION OF THE HORIZONTAL LINE IN PERSPECTIVE.  BECAUSE*
C* THE FIGURE REPRESENTED IS TO BE ROTATED ABOUT THE X-AXIS      *
C* (DEPRESSED) AND THE Z-AXIS (ROTATED), EACH LINE MUST BE RE-   *
C* ORIENTED AS IT IS TO BE DRAWN TO PROVIDE A PERSPECTIVE VIEW.  *
C****************************************************************
C
      INTEGER COLONY,X,Y,Z,EYE,PENNER,UPDOWN,ITERAT
      COMMON/COMDAT/COLONY(50,50)
      COMMON/PLOTDAT/IBUF(513),DIST,ROTATE,DEPRES,ITERAT,ROTAT
      COMMON/SCALE/SCALER
C
C****************************************************************
C*     THE DATA STATEMENT BELOW PROVIDES THE COORDINATES OF THE  *
C* CENTER OF ROTATION.  THE NEXT, "CALL FACTOR," STATEMENT       *
C* PROVIDES THE PLOTTER SOFTWARE WITH INFORMATION ON THE LENGTH  *
C* OF A UNIT INCREMENT.  IF "SCALER" EQUALS ONE, A SINGLE UNIT IS*
C* ONE INCH.                                                     *
C****************************************************************
C
      DATA XCENTER/25./,YCENTER/25./,ZCENTER/30./
      CALL FACTOR(SCALER)
C
C****************************************************************
C*     THIS SUBROUTINE WILL BE CALLED UPON TO DRAW HORIZONTAL    *
C* LINES FOR THREE DIFFERENT PERSPECTIVE VIEWS OF THE SAME SET OF*
C* POINTS IN THE WORKSPACE.  THE FIRST TWO (WHICH OUGHT TO BE    *
C* DEPRESSED ABOUT THE X-AXIS APPROXIMATELY -80. DEGREES) ARE    *
C* DESIGNED TO BE STEREO PAIRS AND CONSEQUENTLY, THE SECOND IS   *
C* ROTATED SIX DEGREES LESS ABOUT THE Z-AXIS THAN THE FIRST.  THE*
C* THIRD PLOT, WHICH IS TO REPRESENT A SINGLE, MORE CASUAL VIEW  *
C* IS DEPRESSED ONLY -60. DEGREES ABOUT THE X-AXIS AND HAS THE   *
C* SAME DEGREE OF ROTATION ABOUT THE Z-AXIS AS THE FIRST PLOT.   *
C****************************************************************
C
      IF(EYE.EQ.2)ROTAT=(ROTATE-6.)*0.01745
      IF(EYE.EQ.3)ROTAT=ROTATE*0.01745
      IF(EYE.EQ.3)DEPRES=-60.*0.01745
C
C****************************************************************
C*     EACH POINT IS TRANSLATED, SO THAT THE POINT OF ROTATION   *
C* BECOMES THE ORIGIN.                                           *
C****************************************************************
C
      XO=FLOAT(X)-XCENTER
      YO=FLOAT(Y)-YCENTER-1
      ZO=FLOAT(Z)-ZCENTER-1
C
C****************************************************************
C*     THE FOLLOWING LOOP EXECUTES TWICE.  THE FIRST TIME, WITH  *
C* PEN UP, THE PLOTTER IS INSTRUCTED TO GO TO THE SITE WHERE THE *
C* HORIZONTAL LINE IS TO BE DRAWN.  THE SECOND TIME, WITH PEN    *
```

```
C* DOWN, THE HORIZONTAL LINE IS DRAWN FROM THE REORIENTED POINT  *
C* TO THE CORRESPONDING POINT WITH ONE UNIT GREATER Y-VALUE,     *
C* SIMILARLY ORIENTED, IN PERSPECTIVE AND PROJECTED ON THE XY-   *
C* PLANE.                                                        *
C*****************************************************************
C
      PENNER=3
      DO 422 UPDOWN=1,2
        IF(UPDOWN.EQ.2)YO=YO+1.
        IF(UPDOWN.EQ.2)PENNER=2
C
C*****************************************************************
C*     THE NEXT THREE STATEMENTS PERFORM THE REORIENTATION OF THE*
C* ENDPOINTS OF THE LINE SEGMENT TO BE DRAWN.                    *
C*****************************************************************
C
        XPRIME=COS(ROTAT)*XO-SIN(ROTAT)*YO
        YPRIME=COS(DEPRES)*SIN(ROTAT)*XO+COS(DEPRES)*COS
     +(ROTAT)*YO-SIN(DEPRES)*ZO
        ZPRIME=SIN(DEPRES)*SIN(ROTAT)*XO+SIN(DEPRES)*COS
     +(ROTAT)*YO+COS(DEPRES)*ZO
C
C*****************************************************************
C*     THE FOLLOWING STATEMENTS PERFORM THE PROJECTION TO THE XY-*
C* PLANE AND THEREBY PROVIDE THE COORDINATES FOR THE PLOTTER.    *
C* THE PARAMETER, "DIST," REPRESENTS THE DISTANCE BETWEEN THE    *
C* VIEWER'S EYE AND THE IMAGE'S CENTER OF ROTATION.  ITS VALUE IS*
C* TRANSFERRED FROM SUBROUTINE "PSTART" WITH OTHER PLOTTING      *
C* INFORMATION THROUGH A COMMON STATEMENT.                       *
C*****************************************************************
C
        XTRANS=XPRIME*DIST/(DIST-ZPRIME)
        YTRANS=YPRIME*DIST/(DIST-ZPRIME)
        CALL PLOT(XTRANS,YTRANS,PENNER)
  422 CONTINUE
      RETURN
      END
C
C
C
      SUBROUTINE VERT(X,Y,Z,EYE)
C
C*****************************************************************
C*     CALLED BY THE MAIN PROGRAM, THIS SUBROUTINE TAKES A SET OF*
C* COORDINATES DEEMED BY THE MAIN PROGRAM TO REPRESENT A VERTICAL*
C* BOUNDARY BETWEEN AN OCCUPIED SPACE AND AN EMPTY SPACE IN THE  *
C* COMPLETED COLONY WORKSPACE AND DRAWS A REPRESENTATION OF THE  *
C* VERTICAL LINE IN PERSPECTIVE.  SEE THE TWIN SUBROUTINE "HORIZ"*
C* FOR FURTHER INFORMATION ON TRANSLATING AND REORIENTING.       *
C*****************************************************************
C
      INTEGER COLONY,X,Y,Z,EYE,PENNER,UPDOWN,ITERAT
      COMMON/COMDAT/COLONY(50,50)
      COMMON/PLOTDAT/IBUF(513),DIST,ROTATE,DEPRES,ITERAT,ROTAT
      COMMON/SCALE/SCALER
      DATA XCENTER/25./,YCENTER/25./,ZCENTER/30./
      CALL FACTOR(SCALER)
      IF(EYE.EQ.2)ROTAT=(ROTATE-6.)*0.01745
      IF(EYE.EQ.3)ROTAT=ROTATE*0.01745
      IF(EYE.EQ.3)DEPRES=-60.*0.01745
      XO=FLOAT(X)-XCENTER
      YO=FLOAT(Y)-YCENTER
      ZO=FLOAT(Z)-ZCENTER-1
C
C*****************************************************************
C*     THE FOLLOWING LOOP EXECUTES TWICE. THE FIRST TIME, WITH   *
C* PEN UP, THE PLOTTER GOES TO THE SITE WHERE THE VERTICAL LINE  *
C* IS TO BE DRAWN.  THE SECOND TIME, WITH PEN DOWN, THE VERTICAL *
C* LINE IS DRAWN FROM THE REORIENTED POINT TO THE CORRESPONDING  *
C* ONE WITH ONE UNIT GREATER Z-VALUE, SIMILARLY REORIENTED, IN   *
C* PERSPECTTIVE, AND PROJECTED ON THE XY-PLANE.  SEE THE TWIN    *
C* SUBROUTINE HORIZ FOR MORE INFORMATION ON THE REORIENTATION AND*
```

```
C* PROJECTION EQUATIONS.                                              *
C**********************************************************************
C
      PENNER=3
      DO 522 UPDOWN=1,2
        IF(UPDOWN.EQ.2)ZO=ZO+1.
        IF(UPDOWN.EQ.2)PENNER=2
C
        XPRIME=COS(ROTAT)*XO-SIN(ROTAT)*YO
        YPRIME=COS(DEPRES)*SIN(ROTAT)*XO+COS(DEPRES)*COS
     +(ROTAT)*YO-SIN(DEPRES)*ZO
        ZPRIME=SIN(DEPRES)*SIN(ROTAT)*XO+SIN(DEPRES)*COS
     +(ROTAT)*YO+COS(DEPRES)*ZO
        XTRANS=XPRIME*DIST/(DIST-ZPRIME)
        YTRANS=YPRIME*DIST/(DIST-ZPRIME)
        CALL PLOT(XTRANS,YTRANS,PENNER)
  522 CONTINUE
      RETURN
      END
C
C
C
C**********************************************************************
C*     THE FOLLOWING LINES REPRESENT A DATA SET DESIGNED TO BE       *
C* READ IN BY THIS PROGRAM.  EACH PARAMETER IS IN THE REQUIRED       *
C* FORMAT AND ORDER.  PARENTHETICAL REMARKS ARE EXPLANATORY.         *
C* THE USER WISHING TO ADAPT THIS PROGRAM AND DATA SET IS            *
C* REMINDED TO USE THE PROPER CONTROL AND DELIMITER CARDS.           *
C**********************************************************************
C
2.00          (THIS SCALING FACTOR MAKES THE PLOT TWICE ACTUAL SIZE)
  THIS LINE TAKES UP THE ENTIRE SPACE ALLOCATED FOR THE TITLE.
11                          (NUMBER OF ITERATIONS)
0010.00000              (DEGREES OF CLOCKWISE ROTATION OF PLOT)
-060.00000         (DEGREES OF DEPRESSION CLOCKWISE ABOUT X-AXIS)
0004.50000             (BRANCH AXIS ENDOZONE EXTENSION RATE)
0001.00000                (ELLIPTIC RADII: X-COMPONENT)
0001.00000        (Y-COMPONENT; SAYING THAT THE ENDOZONE IS CIRCULAR)
0000.20000            (CRITICAL CONCENTRATION OF ENDOZONE MORPHOGEN)
0001.00000          (MAXIMUM CONCENTRATION OF MORPHOGEN AT SOURCE)
0050.00000                (INTRINSIC ANGLE OF BIFURCATION)
0005.00000       (DEGREES OF RANDOM DEVIATION IN BIFURCATION ANGLE)
04                (DISTANCE FROM MORPHOGEN SOURCE TO ITS SINK)
0000.25000 (ITITIAL GROWTH RATE FOR MORPHOGEN CONCENTRATION AT SOURCE)
03                (RECOVERY PERIOD AFTER AN INDIVIDUAL BIFURCATION)
0001.5000       (RANDOM VARIABILITY IN RECOVERY PERIOD; 3 ST. DEV.)
0000.8000           (GROWTH RATE OF BASAL COMMON BUD: X-COMPONENT)
0000.8000            (Y-COMPONENT; NON-DIRECTIONAL INCRUSTATION)
06              (NUMBER OF ITERATIONS BETWEEN EXOZONE AUGMENTATIONS)
0025.00000             (CRITCIAL DISTANCE FOR AUTO-AVOIDANCE)
0005.00000      (CRITCIAL TIP DISTANCE FOR BIFURCATION INHIBITION)
0005.00000  (MAGNITUDE OF AVOIDANCE REACTION, SEE SUBROUTINE "AVOID")
```

AASP

This program is shorter and simpler than DWBBF. Someone wishing to understand the intrinsic code of these programs is advised to study this one first. AASP is designed to aid in the study of mechanisms producing growth patterns in extensively growing colonies constrained to grow in two dimensions. Branches are simulated as line segments; width is not considered. The primary mechanisms included are the extension and dichotomy of branch axes, the modification of branch growth direction using a random component and an auto-avoidance mechanism and a branch-tip proximity-feedback inhibition of bifurcation events. The program furnishes a schematic plot of the colony simulated.

The user accesses and runs the program using the "ATTACH," "USE," and "FTNER" commands to the interactive system. The program resides in the permanent file:

AUTOAVOIDANCESIMULATIONPLOTTER.

After the run is started, the computer prompts and waits for the user to enter values for the following parameters: critical distance for the access to the avoidance mechanism, critical distance to neighboring branch tips for bifurcation inhibition, number of iterations, degree of random play in branch growth direction, and angle of bifurcation. The program maintains certain options for modifications that can be made after the "USE" command is issued, but before the "FTNER."

```
      PROGRAM AVOID(INPUT,OUTPUT)
C
C*****************************************************************
C*      THIS PROGRAM OPERATES INTERACTIVELY.                      *
C*      THIS PROGRAM IS DESIGNED TO SIMULATE THE EXTENDED GROWTH  *
C* OF BRYOZOAN COLONIES CONSTRAINED TO GROW IN THE XY-PLANE.      *
C* PARAMETERS ARE READ IN FOR VARIOUS GROWTH AND ANTI-ANASTOMOSIS*
C* MECHANISMS.                                                    *
C*****************************************************************
C
      INTEGER NAXES,KAXES,NZOIDS,ITERS
      REAL AXIS(200,2),BASE(200,2),TIP(200,2),CRDIST,BFDIST,PI,DIST,
     +PHI,PLAY,NORM,ANGLE,ZOID(2000,2),RNF,RANDND
      DIMENSION IBUF(257)
  111 CONTINUE
C
C*****************************************************************
C*      THIS STATEMENT SETS UP THE PLOT ON MSU'S CALCOMP SYSTEM.  *
C* THE LAST NUMBER INDICATES THE TYPE OF PENS AND PAPER.  FOR     *
C* FURTHER INFORMATION, SEE MSU'S COMPUTER GRAPHICS REFERENCE     *
C* MANUAL.                                                        *
C*****************************************************************
C
        CALL PLOTS(IBUF,257,0)
        CALL PLOT(6.0,6.0,-3)
C
C*****************************************************************
C*      THIS STATEMENT SETS UP THE SCALING FOR THE PLOT WHERE ONE *
C* UNIT DISTANCE IS EXPRESSED IN TERMS OF AN INCH.  FOR A PLOT    *
C* UNIT OF ONE MILLIMETER, A "CALL FACTOR(0.0394)" IS USED.       *
C* FOR A PLOT UNIT OF A CENTIMETER, A "CALL FACTOR(0.394)" IS     *
C* USED.                                                          *
C*****************************************************************
C
        CALL FACTOR(0.0985)
C
C*****************************************************************
C*      "CRDIST" IS THE DISTANCE BEYOND WHICH A PARTICULAR REPRE- *
C* SENTATIVE OF A COLONY PART WILL NOT BE CONSIDERED IN THE       *
C* AVOIDANCE RESPONSE FOR A SPECIFIC BRANCH.                      *
C*****************************************************************
C
        PRINT*,"CRITICAL AVOIDANCE DISTANCE?"
        READ 2,CRDIST
      2 FORMAT(F10.5)
C
C*****************************************************************
C*      "BFDIST" IS THE MAXIMUM DISTANCE AT WHICH THE PROXIMITY OF*
C* A BRANCH TIP WILL INHIBIT THE BIFURCATION OF ANOTHER.          *
C*****************************************************************
C
        PRINT*,"BIFURCATION INHIBITION DISTANCE?"
        READ 2,BFDIST
        PRINT*,"NUMBER OF ITERATIONS?"
        READ 6,ITERS
      6 FORMAT(I3)
C
C*****************************************************************
C       "PLAY" REPRESENTS THREE STANDARD DEVIATIONS OF NORMALLY   *
C* DISTRIBUTED VARIATION AROUND A BRANCH'S GROWTH DIRECTION.  THE*
C* NUMBER IS DIVIDED BY THE NUMBER OF DEGREES IN A RADIAN HERE    *
C* BECAUSE THE TRIGONOMETRIC FUNCTIONS THAT FOLLOW REQUIRE ARGU-  *
C* MENTS IN TERMS OF RADIANS.                                     *
C*****************************************************************
C
        PRINT*,"DEGREES OF RANDOM PLAY IN BRANCH DIRECTION?"
        READ 2,PLAY
        PLAY=PLAY/57.3
        PRINT*,"ANGLE OF BIFURCATION?"
        READ 2,ANGLE
C
C*****************************************************************
```

```
C*     THE ANGLE OF BIFURCATION IS DIVIDED BY THE NUMBER OF         *
C* DEGREES HERE BECAUSE THE FOLLOWING TRIGONOMETRIC FUNCTIONS       *
C* REQUIRE ARGUMENTS IN TERMS OF RADIANS.                           *
C*******************************************************************
C
       ANGLE=ANGLE/57.3
C
C*******************************************************************
C*     THE FOLLOWING STATEMENT INITIALIZES THE NUMBER OF AXES AT *
C* THE BEGINNING OF THE RUN.                                        *
C*******************************************************************
C
       NAXES=5
       PI=3.1416
C
C*******************************************************************
C*     THE FOLLOWING LOOP ASSIGNS VECTOR DIRECTIONS FOR THE FIVE *
C* INITIAL AXES, SPREAD A CERTAIN AMOUNT AROUND A CIRCLE.           *
C*     "FAX/18." RESTRICTS ALL FIVE INITIAL AXES TO EIGHTY          *
C* DEGREES OF ARC. "FAX/5." GIVES ALL FIVE INITIAL AXES AN EVEN  *
C* SPREAD AROUND A FULL CIRCLE.                                     *
C*******************************************************************
C
       DO 11 IAX=1,5
         FAX=FLOAT(IAX)
         AXIS(IAX,1)=COS((FAX/5.)*(2.*PI))
         AXIS(IAX,2)=SIN((FAX/5.)*(2.*PI))
   11  CONTINUE
C
C*******************************************************************
C*     THE FOLLOWING LOOP SETS THE INITIAL BASE AND BRANCH TIP     *
C* COORDINATES FOR THE FIVE NEW AXES.                               *
C*******************************************************************
C
       DO 22 IA=1,5
         DO 21 IB=1,2
           BASE(IA,IB)=0.0000
           TIP(IA,IB)=0.0000
   21    CONTINUE
   22  CONTINUE
C
C*******************************************************************
C*     THIS STATEMENT SETS THE INITIAL NUMBER OF "REPS" (WHICH     *
C* ARE INDIVIDUAL POINTS WITHIN COLONY PARTS REPRESENTING THE       *
C* POSITIONS OF THOSE PARTS FOR POSSIBLE USE WITH THE AVOIDANCE    *
C* MECHANISM) TO ZERO.                                              *
C*******************************************************************
C
       NZOIDS=0
C
C*******************************************************************
C*     IN THIS LOOP, ONE ITERATION AT A TIME, EACH OF THE          *
C* EXISTING AXES ARE LENGTHENED ACCORDING TO THEIR ASSIGNED AND    *
C* MODIFIED GROWTH VECTORS, REPRESENTATIVE POINTS ARE RECORDED,    *
C* AXES ARE INITIATED, AND GROWTH VECTORS ARE MODIFIED FOR THE     *
C* NEXT ITERATION.                                                  *
C*******************************************************************
C
       DO 401 I=1,ITERS
         KAXES=NAXES
C
C*******************************************************************
C*     THIS LOOP, WHICH IS CONTAINED INSIDE THE PREVIOUS ONE,      *
C* GOES THROUGH EACH AXIS EXISTING BY THE END OF THE PREVIOUS      *
C* ITERATION, MODIFIES THE DIRECTIONAL COMPONENT OF ITS GROWTH     *
C* VECTOR BASED ON A RANDOM FACTOR WITH A PREDETERMINED AMOUNT     *
C* OF PLAY, INCREASES THE AXIS' LENGTH BY A SINGLE INCREMENT,      *
C* RECORDS THE REPRESENTATIVE ZOOID'S LOCATION, DETERMINES THE     *
C* DISTANCE BETWEEN TIPS AND ASSIGNS GROWTH VECTORS TO NEWLY       *
C* INITIATED AXES THEREBY DETERMINED.                               *
C*******************************************************************
C
```

```
          DO 101 K=1,KAXES
            PHI=ACOS(AXIS(K,1))
            IF(AXIS(K,2).LT.O.)PHI=-PHI
            RANDND=SQRT(-2.*ALOG(RANF(X)))*SIN(6.2832*RANF(X))
            PHI=PHI+(RANDND*(PLAY/3.))
            AXIS(K,1)=COS(PHI)
            AXIS(K,2)=SIN(PHI)
            BASE(K,1)=TIP(K,1)
            BASE(K,2)=TIP(K,2)
            TIP(K,1)=TIP(K,1)+AXIS(K,1)
            TIP(K,2)=TIP(K,2)+AXIS(K,2)
C
C*****************************************************************
C*     THE FOLLOWING STATEMENT INCREASES THE NUMBER OF           *
C* REPRESENTATIVE ZOOIDS TO ACCOUNT FOR NEWLY ADDED COLONY PARTS.*
C*****************************************************************
C
            NZOIDS=NZOIDS+1
            ZOID(NZOIDS,1)=TIP(K,1)
            ZOID(NZOIDS,2)=TIP(K,2)
C
C*****************************************************************
C*     IF THE NUMBER OF REPRESENTATIVE ZOOIDS REACHES THE 2000   *
C* ZOOID LIMIT, THE FOLLOWING STATEMENT AUTOMATICALLY STOPS THE  *
C* PROGRAM.                                                      *
C*****************************************************************
C
            IF(NZOIDS.EQ.2000)GO TO 444
C
C*****************************************************************
C*     THE FOLLOWING LOOP, WHICH IS FULLY CONTAINED IN THE TWO   *
C* PRECEDING ONES, MAKES NEW AXES BASED ON DISTANCE FROM THE     *
C* TIPS OF NEIGHBORING AXES TO THE ONE BEING CONSIDERED.  WHEN   *
C* THE TIP OF THE AXIS IS GREATER THAN A CRITICAL DISTANCE FROM  *
C* ANY OTHER AXIS, THE PROGRAM ASSIGNS TWO NEW DIRECTIONS (ONE   *
C* TO EACH OF THE NEW BRANCH TIPS) BASED ON THE GROWTH VECTOR OF *
C* THE PARENT AXIS AND THE PREDETERMINED ANGLE OF BIFURCATION.   *
C*****************************************************************
C
            DO 90 KA=1,KAXES
              IF(K.EQ.KA)GO TO 90
                DIST=SQRT((TIP(KA,1)-TIP(K,1))**2.+(TIP(KA,2)-
     +TIP(K,2))**2.)
C
C*****************************************************************
C*     IF THE BRANCH TIP BEING CONSIDERED FOR BIFURCATION IS TOO *
C* CLOSE TO ANOTHER TIP, THE NEXT STATEMENT EJECTS TO THE OUTER  *
C* LOOP.                                                         *
C*****************************************************************
C
                IF(DIST.LT.BFDIST)GO TO 91
                IF(KA.LT.KAXES)GO TO 90
C
C*****************************************************************
C*     THE FOLLOWING STATEMENTS INCREASE THE NUMBER OF AXES,     *
C* INITIALIZE THE NEW AXIS, AND MODIFY THE GROWTH VECTOR OF THE  *
C* PARENT TO SIMULATE A BIFURCATION.                             *
C*****************************************************************
C
                  NAXES=NAXES+1
                  TIP(NAXES,1)=TIP(K,1)
                  TIP(NAXES,2)=TIP(K,2)
                  BASE(NAXES,1)=TIP(K,1)
                  BASE(NAXES,2)=TIP(K,2)
                  AXIS(NAXES,1)=COS(PHI+ANGLE/2.)
                  AXIS(NAXES,2)=SIN(PHI+ANGLE/2.)
                  AXIS(K,1)=COS(PHI-ANGLE/2.)
                  AXIS(K,2)=SIN(PHI-ANGLE/2.)
   90       CONTINUE
C
C*****************************************************************
C*     HERE THE INNERMOST LOOP HAS ENDED.                        *
```

```
C*****************************************************************
C
   91       CONTINUE
  101     CONTINUE
C
C*****************************************************************
C*     HERE THE FIRST INNER LOOP HAS ENDED.                       *
C*****************************************************************
C
C*****************************************************************
C*     HERE THE SECOND INNER LOOP, COMPLETELY CONTAINED IN THE    *
C* OUTERMOST LOOP, BEGINS.  IT GOES THROUGH EACH AXIS AND         *
C* MODIFIES THE DIRECTIONAL COMPONENTS OF ITS GROWTH VECTORS      *
C* BASED ON THE PROXIMITY OF NEIGHBORING COLONY PARTS TO BE       *
C* AVOIDED.                                                       *
C*****************************************************************
C
          DO 201 L=1,NAXES
C
C*****************************************************************
C*     THE FOLLOWING LOOP, FULLY WITHIN THE SECOND INNER LOOP,    *
C* GOES THROUGH ALL REPRESENTATIVE ZOOIDS AND COMPUTES DISTANCE   *
C* TO THE TIP UNDER CONSIDERATION AND ADDS UNIT VECTORS (WEIGHTED*
C* FOR PROXIMITY) TO THE AXIS' GROWTH VECTOR AT ITS TIP.  THE     *
C* RESULT OF DIVIDING THIS SUM BY ITS NORM IS A NEW UNIT VECTOR   *
C* WHICH REFLECTS THE AVOIDANCE RESPONSE OF THE GROWING TIP TO    *
C* THE POSITIONS OF REPRESENTATIVE ZOOIDS WITHIN THE CRITICAL     *
C* DISTANCE.                                                      *
C*****************************************************************
C
            DO 190 LA=1,NZOIDS
              DIST=SQRT((ZOID(LA,1)-TIP(L,1))**2.+(ZOID(LA,2)-TIP
     +(L,2))**2.)
              IF((DIST.GT.CRDIST).OR.(DIST.EQ.O.))GO TO 190
                AXIS(L,1)=AXIS(L,1)+(TIP(L,1)-ZOID(LA,1))/DIST**2.
                AXIS(L,2)=AXIS(L,2)+(TIP(L,2)-ZOID(LA,2))/DIST**2.
  190       CONTINUE
C
C*****************************************************************
C*     HERE THE INNERMOST LOOP HAS ENDED.                         *
C*****************************************************************
C
            NORM=SQRT(AXIS(L,1)**2.+AXIS(L,2)**2.)
            AXIS(L,1)=AXIS(L,1)/NORM
            AXIS(L,2)=AXIS(L,2)/NORM
C
C*****************************************************************
C*     THESE NEXT TWO STATEMENTS TELL THE PLOTTER, RESPECTIVELY, *
C* TO GO TO THE SITE OF THE NEWLY GROWN SECTION OF BRANCH AND     *
C* THEN TO DRAW A LINE SEGMENT CORRESPONDING TO THE NEW GROWTH.  *
C*****************************************************************
C
            CALL PLOT(BASE(L,1),BASE(L,2),3)
            CALL PLOT(TIP(L,1),TIP(L,2),2)
C
C*****************************************************************
C*     HERE ENDS THE SECOND INNER LOOP.                           *
C*****************************************************************
C
  201     CONTINUE
C
C*****************************************************************
C*     HERE ENDS THE OUTERMOST LOOP.                              *
C*****************************************************************
C
  401   CONTINUE
  444   CONTINUE
        CALL PLOT(36.0,0.0,999)
        PRINT*,"DO YOU WISH TO CONTINUE? Y OR N---"
        READ 4,ANS
    4   FORMAT(A1)
      IF(ANS.EQ.1HY)GO TO 111
```

```
STOP
END
```

BBK

The following algorithm (called BBK in the text) is a modification for DWBBF that may be used in situations wherein the shape of individual zooids is an important factor in the shape of the colony. It is designed to replace the code which causes a cylindrical branch segment to be drawn. Instead of the cylindrical, one with nodes, corresponding to the caudal portions of individual zooids, is constructed. This is done by replacing the limiting formula of an elliptical cylinder for that of an elliptical paraboloid. Note that the shape of bead-like zooids can be simulated using the formulas for various ellipsoids. In the algorithm listed here, the proximal truncating plane, used to trim the cylinder in DWBBF, is used to exclude the paraboloid's negative twin. The contents of the algorithm replace the contents of the nested "DO-loops" ending with statement number "653." The values of the coordinates of the base and tip of the previously grown branch segment, the components of the branch's growth vector, and the elliptical components of the parabolic section are provided before the loops are entered. Notice that the endozone width is not considered in the growth of the branch and other references to it in DWBBF can be ommitted if the modification is made. The shape of the zooid is determined by the endozone extension rate and the elliptical components of the parabolic equation.

.
.
.

```
C
C*****************************************************************
C*     THIS PART OF THE MODIFICATION SHOULD BE PLACED WITH THE   *
C* "READ" STATEMENTS AT THE BEGINNING OF SUBROUTINE "GROWER."    *
C*     THE FOLLOWING TWO PARAMETERS ARE DESIGNED TO HELP PROVIDE *
C* A VARIETY OF ZOOECIAL SHAPES FOR THE INTERNODAL PORTIONS OF   *
C* UNISERIAL BRANCHES.  BECAUSE THE BASIC SHAPE IN THIS VERSION  *
C* IS A PARABOLOID, VARYING THE TWO PARAMETERS WILL PRODUCE      *
C* VARIOUSLY SHAPED PARABOLOIDS.  IF "COEF" AND "EXP" ARE BOTH   *
C* SET TO 1.0, A STANDARD (Z=X**2/H**2+Y**2/KAY**2), ALBEIT      *
C* REORIENTED, PARABOLOID RESULTS.  DECREASING OR INCREASING     *
C* "COEF" PRODUCES A NARROWER OR SQUATTER PARABOLOID,            *
C* RESPECTIVELY.  IF "EXP" IS DECREASED, A NARROWER PARABOLOID   *
C* WITH A BLUNTER BASE RESULTS.  IF "EXP" IS SET TO 2.0, A       *
C* STRAIGHT-SIDED CONE IS PRODUCED. "EXP" GREATER THAN 2.0       *
C* RESULTS IN A ZOOECIUM WITH CONCAVE SIDES.                     *
C*****************************************************************
C
      READ(60,7001)COEF
 7001 FORMAT(F10.5)
      WRITE(61,7002)COEF
 7002 FORMAT(* ZOOECIAL SHAPE; COEFFICIENT FOR PARABOLOID: *,F10.5)
      READ(60,7001)EXP
      WRITE(61,7003)EXP
 7003 FORMAT(* ZOOECIAL SHAPE; EXPONENT FOR PARABOLOID: *,F10.5)
```

.
.
.

```
C
C*****************************************************************
C*     THE REMAINER OF THIS MODIFICATION LIES WITHIN THE SET OF  *
C* THREE NESTED LOOPS ENDING WITH STATEMENT NUMBER 653.          *
C*     THE FOLLOWING SET OF NESTED LOOPS SERVES TO RECORD THE    *
C* BRANCH'S ENDOZONAL GROWTH INTO THE COLONY WORKSPACE.  EACH     *
C* POINT IN THE WORKSPACE IS INDIVIDUALLY TESTED FOR INCLUSION.  *
C*****************************************************************
C
          DO 653 I=1,50
            DO 652 J=1,50
              DO 651 L=1,50
C
C*****************************************************************
C*     THE FOLLOWING ASSIGNMENTS ARE MADE WITH THE HOPE OF       *
C* RENDERING THE CALCULATIONS THAT FOLLOW LESS CLUTTERED.        *
C*****************************************************************
C
                X=FLOAT(I)
                Y=FLOAT(J)
                Z=FLOAT(K)
                TX=TIP(N,1)
                TY=TIP(N,2)
                TZ=TIP(N,3)
                XP=BASE(N,1)
                YP=BASE(N,2)
                ZP=BASE(N,3)
                A=AXIS(N,1)
                B=AXIS(N,2)
                C=AXIS(N,3)
C
C*****************************************************************
C*     THE NEWLY GROWN PART OF EACH BRANCH IS SIMULATED AS A     *
C* TRUNCATED PARABOLOID ADDED ON TO THE PREVIOUS BRANCH TIP.     *
C* THE POINTS, CORRESPONDING TO THIS PARABOLOID, WHICH WILL BE   *
C* ADDED TO THE COLONY IMAGE IN THE WORKSPACE, ARE BOUNDED BY THE*
C* PARABOLOID, ORIENTED IN THREE-SPACE, A PAIR OF PARALLEL PLAINS*
C* WHICH ARE NORMAL TO THE DIRECTRIX OF THE PARABOLOID (THE      *
C* GROWTH DIRECTION), AND COINCIDENT WITH THE OLD AND NEW POSI-  *
C* TIONS OF THE BRANCH TIP.  THE TWO STATEMENTS FOLLOWING WILL   *
C* ELIMINATE FROM CONSIDERATION ALL POINTS THAT DO NOT LIE       *
```

```
C* BETWEEN THESE PLANES FOR ANY GIVEN BRANCH AXIS.                  *
C*******************************************************************
C
               IF((A*(X-TX)+B*(Y-TY)+C*(Z-TZ)).LT.O.)GO TO 651
               IF((A*(X-(TX+A))+B*(Y-(TY+B))+C*(Z-(TZ+C))).GT.
     +O.)GO TO 651
C
C*******************************************************************
C*     THE FOLLOWING SET OF TRANSFORMATIONS AND IF-STATEMENT WILL*
C* ELIMINATE POINTS NOT FOUND WITHIN THE PARABOLOID FROM            *
C* CONSIDERATON FOR INCLUSION IN THE WORKSPACE.                     *
C*******************************************************************
C
                 PSI=ASIN(AXIS(N,1)/GR)
                 CHI=ACOS(AXIS(N,3)/(COS(PSI)*GR))
                 IF(AXIS(N,2).GT.O.O)CHI=-CHI
                 XTERM=(X-TX)*COS(PSI)+(Y-TY)*SIN(CHI)*SIN(PSI)
     +-(Z-TZ)*COS(CHI)*SIN(PSI)
                 YTERM=(Y-TY)*COS(CHI)+(Z-TZ)*SIN(CHI)
                 ZTERM=(X-TX)*SIN(PSI)-(Y-TY)*SIN(CHI)*COS(CHI)
     ++(Z-TZ)*COS(CHI)*COS(PSI)
                 IF(ZTERM.EQ.O.)ZTERM=O.OOOO1
                 IF((XTERM**2/H**2+YTERM**2/KAY**2).GT.COEF*(ABS(
     +ZTERM))**EXP)GO TO 651
C
C*******************************************************************
C*     IF A POINT(I,J,L) IS FOUND TO BE INCLUDED IN THE NEWLY      *
C* GROWN BRANCH SEGMENT, IT IS ADDED TO THE IMAGE IN THE            *
C* WORKSPACE BY THE FOLLOWING ALGORITHM.  THE L-COORDINATE IS THE*
C* HEIGHT (CORRESPONDING TO Z-VALUES IN THE WORKSPACE).  AN         *
C* INTEGER WORD IS INITIATED, WHICH HAS THE FIRST FIFTY-NINE BITS*
C* SET TO ZERO AND THE SIXTIETH BIT SET TO ONE, REPRESENTING AN  *
C* ERECT COLUMN SIXTY BITS HIGH WITH THE BOTTOM-MOST UNIT FILLED *
C* AND ALL ABOVE IT UNOCCUPIED.  THE "SHIFT" OPERATION, AVAILABLE*
C* ON THE MICHIGAN STATE UNIVERSITY COMPUTER SYSTEM, IS USED TO  *
C* MOVE THE FILLED BIT TO THE LEFT IN THE INTEGER WORD, FROM THE *
C* LAST (ZERO HEIGHT OR SIXTIETH) POSITION TO A POSITION          *
C* CORRESPONDING TO THE HEIGHT OF THE L-COORDINATE.  THE ".OR."  *
C* OPERATION THEN ADDS THIS FILLED BIT TO THE WORD IN THE          *
C* WORKSPACE HOLDING ALL THE POINTS WITH X- AND Y-COORDINATES     *
C* CORRESPONDING TO THE CURRENT VALUES OF J AND K.                 *
C*******************************************************************
C
                   IHT=L
                   IMASK=MASK(1)
                   INCMNT=SHIFT(IMASK,IHT)
                   COLONY(I,J)=COLONY(I,J).OR.INCMNT
  651          CONTINUE
  652        CONTINUE
  653      CONTINUE
                      .
                      .
                      .
```

# APPENDIX II

## TESTING POINTS IN A THREE-DIMENSIONAL WORKSPACE FOR INCLUSION IN A GROWING BRANCH TIP

The growth of a stem can be seen as a vector in three-space. The growth rate is represented by the vector's magnitude. For each iteration in a growth simulation, new material must be added onto the tip of the growing branch in the same direction as the vector.

The branch may be seen as a cylinder with a specific orientation (eg. a circle, an ellipse, or any closed figure). As the simulated branch grows, points in the workspace are added to the colony when they are included inside the currently grown cylinder segments.

Points can be tested for inclusion in a specific branch segment by comparing them to the formula for the cylinder, the plane normal to the growth vector at the branch tip position before starting the iteration's growth, and the plane normal to the growth vector at the branch tip position after the iteration's growth.

A vertical cylinder may be described by the formula for its intersection with the XY-plane. For example, the same equation that describes a circle in two-space, describes a vertical circular cylinder in three-space. If the coordinates are closer to the axis than points on the cylinder's surface, the point will rest within the cylinder.

If this vertical cylinder were to be translated to the site of the branch tip and rotated about various axes to bring its long axis to coincide with the growth vector, a set of points might be tested for inclusion in it. However, it is much easier to test for inclusion in a vertical cylinder: If the X and Y coordinates of the point lie within the cylinder's transverse section, the point can be included in the cylinder. This involves translating each point tested from its position relative to the growing tip, to the equivalent position relative to the origin, finding the angles of rotation between the growth vector and the Z-axis, and then comparing the point's new (translated and rotated) X and Y coordinates to the equation for the cylinder's cross-section. If the translated and rotated point sits within the vertical cylinder, then the original point sits in the equivalent position within the growing branch cylinder.

For the purposes of memory storage and retrieval, output interpretation, and extension of axes, it was found to be most convenient to store the growth vectors in terms of Cartesian coordinates. However, for the purpose of facilitating the simulation of bifurcation, the direction of the growth vector is expressed in terms of a variation on standard spherical coordinates based on the initial plane of dichotomy, parallel to the X-axis. Thus, the direction of growth is described using the vector's norm and two angles. The first angle is "PSI," measured from the YZ-plane to the growth vector. The second is the angle measured from the XY-plane to the plane defined by the vector and the X-axis, "CHI." As with standard spherical coordinates, counterclockwise rotation is considered positive. PSI is found by taking the arcsine of the quantity produced by dividing the X-component of the growth vector by the vector's magnitude. CHI is the arccosine of the quantity produced by dividing the Z-Component of the growth vector by the product of the cosine of PSI and the magnitude of the growth vector. This is then multiplied by -1. if the Y-component of the growth vector is positive.

A point to be tested for inclusion in a growing branch axis must, after translation, be rotated backwards about the X-axis, through an angle of CHI to bring it into its proper position relative to the XZ-plane. Then it must be rotated backwards about the Y-axis, through an angle of PSI, until the growth vector is vertical and the point has reached its proper orientation with respect to the Z-axis. For this purpose, the following matrices can be used:

1. Rotation of a point backward (clockwise, for a positive angle) through the angle CHI about the X-axis:

$$\begin{bmatrix} 1 & 0 & 0 \\ 0 & \cos(CHI) & \sin(CHI) \\ 0 & -\sin(CHI) & \cos(CHI) \end{bmatrix}$$

(This will bring the growth vector into the XZ-plane.)

2. Rotation of a point backward through the angle PSI about the Y-axis:

$$\begin{bmatrix} \cos(PSI) & 0 & -\sin(PSI) \\ 0 & 1 & 0 \\ \sin(PSI) & 0 & \cos(PSI) \end{bmatrix}$$

(This will bring the growth vector into a vertical alignment.)

Given a point to be tested, the X-, Y-, Z-values of the coordinates of the branch tip are first subtracted from the corresponding values of the point's coordinates. These translated coordinates are represented by "x'," "y'," and "z'" in the column natrix to the right (below). The coordinate values of the rotational point are represented by "x," "y," and "z" in the column-matrix product to the left:

$$\begin{bmatrix} x \\ y \\ z \end{bmatrix} = \begin{bmatrix} \cos(PSI) & 0 & -\sin(PSI) \\ 0 & 1 & 0 \\ \sin(PSI) & 0 & \cos(PSI) \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ 0 & \cos(CHI) & \sin(CHI) \\ 0 & -\sin(CHI) & \cos(CHI) \end{bmatrix} \begin{bmatrix} x' \\ y' \\ z' \end{bmatrix}$$

$$= \begin{bmatrix} \cos(PSI) & \sin(CHI)\sin(PSI) & -\cos(CHI)\sin(PSI) \\ 0 & \cos(CHI) & \sin(CHI) \\ \sin(PSI) & -\sin(CHI)\cos(PSI) & \cos(CHI)\cos(PSI) \end{bmatrix} \begin{bmatrix} x' \\ y' \\ z' \end{bmatrix}$$

$$x = x'\cos(PSI) + y'\sin(CHI)\sin(PSI) - z'\cos(CHI)\sin(PSI)$$

$$y = y'\cos(CHI) + z'\sin(CHI)$$

$$z = x'\sin(PSI) - y'\sin(CHI)\cos(PSI) + z'\cos(CHI)\cos(PSI)$$

"x" and "y" can then be used in the following statement to be tested for inclusion in an elliptical branch segment:

```
IF ((X**2/H**2+Y**2/KAY**2).GT.1.)GO TO 651
```

See the program DWBBF (Appendix I) for the application to an algorithm and see also BBK (Appendix I) for an alternative to the cylindrical test equation that tests rather for elliptical paraboloids.

HOW TO ADD RANDOM COMPONENTS TO A VECTOR IN SPACE

A vector in space can be expressed in terms of a norm "$\rho$" and spherical coordinates "$\phi$ and $\theta$." This vector is composed of deterministic components. Stochastic components can be added in terms of additional spherical coordinates, forming a new, stochastic vector. These include the normally distributed deviant angle "$\phi'$" between the new vector and its deterministic component and the uniformly distributed direction of deviation to the new vector from its deterministic components "$\theta'$." $\theta'$ is measured in a counterclockwise direction from the half-plane formed by the vector comprising the deterministic components and the vertical direction. The vector described by these five components (three deterministic, two stochastic) can be transformed into the Cartesian system with the following set of equations.

$$x = \rho\cos\phi'\cos\theta\sin\phi + \rho\sin\phi'(\sin\theta'\sin\theta - \cos\theta'\cos\theta\cos\phi)$$

$$y = \rho\cos\phi'\sin\theta\sin\phi + \rho\sin\phi'(-\sin\theta'\cos\theta - \cos\theta'\sin\theta\cos\phi)$$

$$z = \rho\cos\phi'\cos\phi + \rho\sin\phi'\cos\theta'\sin\phi$$

Notice that for all three coordinates, the contribution of the deterministic components is decreased as the angle of deviation, $\phi'$, increases, while the effect of the random components increases with the angle of deviation. The effects of the random components are further determined, in all three coordinates, by a factor that depends on the latitude and longitude of the vector comprising the vector's deterministic components. In addition, the x and y coordinates' random component is also partly determined by a factor that depends solely on the longitude of the vector's deterministic components, and is independent of latitude.

## ORIENTING AN IMAGE IN SPACE BY ROTATING ABOUT THE X- AND Z-AXES

The coordinates of sets of points can be used to make computer-drawn perspective diagrams. This involves rotating the image into the proper orientation by transforming the coordinates of the image's constituent points, and then projecting the image onto the XY-plane.

First, the coordinates are translated so that the point of rotation becomes the origin. This is done by subtracting the values of the coordinates of the point of rotation from the values of the coordinates of each point. Then the translated points are rotated the desired amount about the vertical Z-axis, which is the line of sight. The following matrix is used. "$\rho$" is the angle of counterclockwise rotation about the Z-axis.

$$\begin{bmatrix} x \\ y \\ z \end{bmatrix} = \begin{bmatrix} \cos\rho & -\sin\rho & 0 \\ \sin\rho & \cos\rho & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} x' \\ y' \\ z' \end{bmatrix}$$

Next the rotated points may be depressed about the X-axis. For this, the following matrix is used, when "$\delta$" is the angle of counterclockwise rotation about the X-axis.

$$\begin{bmatrix} 1 & 0 & 0 \\ 0 & \cos\delta & -\sin\delta \\ 0 & \sin\delta & \cos\delta \end{bmatrix}$$

These matrices may be combined and multiplied out to give equations.

$$\begin{bmatrix} x \\ y \\ z \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & \cos\delta & -\sin\delta \\ 0 & \sin\delta & \cos\delta \end{bmatrix} \begin{bmatrix} \cos\rho & -\sin\rho & 0 \\ \sin\rho & \cos\rho & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} x' \\ y' \\ z' \end{bmatrix}$$

$$= \begin{bmatrix} \cos\rho & -\sin\rho & 0 \\ \cos\delta\sin\rho & \cos\delta\cos\rho & -\sin\delta \\ \sin\delta\sin\rho & \sin\delta\cos\rho & \cos\delta \end{bmatrix} \begin{bmatrix} x' \\ y' \\ z' \end{bmatrix}$$

$$x = x'\cos\rho - y'\sin\rho$$

$$y = x'\cos\delta\sin\rho + y'\cos\delta\cos\rho - z'\sin\delta$$

$$z = x'\sin\delta\sin\rho + y'\sin\delta\cos\rho + z'\cos\delta$$

These points can then be projected onto the XY-plane using the transformed coordinates and the distance "d" between the eye of the viewer and the center of rotation.

$$x'' = (x * d)/(d - z)$$

$$Y'' = (y * d)/(d - z)$$

The result of this projection will be perspective plotting of the points, with the distances between points that are closer to the eye of the viewer drawn relatively larger than those farther away.

# APPENDIX III

## ALGORITHMS FOR GENERATING VARIOUS DISTRIBUTIONS OF RAMDOM NUMBERS

The following FORTRAN algorithms were found to be useful in the simulation of random variation around growth vectors or variation in the timing of developmental events. Each is adapted to be used in conjunction with a machine which has a random number generator capable of producing a uniform continuous distribution from 0. to 1. "RANF(X)" is the built-in function that will supply this initial number in the listings herein. Systems without a random number generator will need an additional algorithm.

The first algorithm will take two uniformly distributed random numbers, RANF(X), between 0. and 1. and transform them to a normal distibution with a desired mean and standard deviation. This is Box and Muller's (1958) "Normal Deviate Tranformation."

$$x = (-2.\ln(U_1))^{.5}\cos(2.\Pi U_2)$$

where $U_1$ and $U_2$ are the random values taken from a uniform distribution (0. to 1.) and x is a random number taken from a normal distribution of mean "0." and standard devaition "1." (This is actually one of a pair of equations. Lewis (1975) gives a "Minnesota" FORTRAN algorithm using both.)

The FORTRAN algorithm used in this study needs, in addition to the supplied variables of mean, standard deviation, and the two uniformly distributed random numbers, certain special functions. These are natural logarithm, square root, and cosine. It is assumed that the built-in uniform random number generator will, if called twice, produce two different random numbers, even in a single line of code. All variables are type REAL.

```
RANSTD=SQRT(-2.*ALOG(RANF(X)))*COS(2.*3.1416*RANF(X))
```

"RANDSTD" is a number chosen from the standard normal distribution, with mean 0. and a standard deviation of 1. The reverse of the z-transform can change this number to another, "RANDND," taken from a distribution with the desired mean, "MU," and standard deviation, "SIGMA."

```
RANDND=(RANDSTD*SIGMA)+MU
```

Box and Muller's Transformation is very accurate and reliable, even in the tails of the distribution. For this reason, it is preferred in the simulation of the timing of threshold-controlled events.

The next algorithm comes directly from Lewis (1975, pg. 68) and is based on the Kahn approximation to the normal distribution. This technique uses only the supplied random number from a uniform distribution from 0. to 1. and the natural logarithm function. It supplies a random number chosen from a normal distribution with mean 0. and standard deviation 1. It is reported not to be reliable in the tails and therefore should not be used where high accuracy is required. It was used to simulate the absolute deviation component of the random variation in branch growth direction in program DWBBF. (Box and Muller's transformation was used, however, in AASP because there were more iterations and often a higher frequency of branching and consequently, a higher demand on the distribution, requiring more use of the tail regions.) All variables are type REAL.

```
RNF=RANF(X)
RANDND=.62666*ALOG((1.+RNF)/(1.-RNF))
```

Finally, there is a Poisson-distributed random-number algorithm that is based upon another derivation by Lewis (1975, pg. 72, note error in final step). "$\lambda$" is the expected value (mean) of the Poisson distribution, "n" is the number of events occurring within a given interval, and each "$r_i$" is a number chosen at random from a continuous uniform distribution from 0. to 1.;

$$e^{-\lambda} \geq \prod_{i=1}^{n+1} r_i .$$

In the algorithm, the expected value, "LAMBDA," is supplied by the user, the uniformly distributed random numbers, "R," are supplied by the function "RANF(X)," and the result, "N," can be considered as an integer chosen at random from a Poisson distribution. LAMBDA, EXNEGL, and R are type REAL. N is type INTEGER. This algorithm may be valuable in the simulation of the occurrence of successive events, such as the timing between dichotomies.

.
.
.

```
C
C*******************************************************************
C*      THIS ALGORITHM PRODUCES A LIST OF TWENTY RANDOM DEVIATES   *
C* TAKEN FROM A POISSON DISTRIBUTION.                               *
C*******************************************************************
C
      READ(60,1)LAMBDA
    1 FORMAT(F10.5)
      EXNEGL=EXP(-1*LAMBDA)
      DO 9999 I=1,20
C
C*******************************************************************
C*       VARIABLE "R" HOLDS THE VALUES OF SUBSEQUENT PRODUCTS OF   *
C* THE UNIFORM RANDOM NUMBERS PRODUCED BY RANF(X).                  *
C*******************************************************************
C
        R=1
        N=-1
 1616   CONTINUE
          R=R*RANF(X)
          N=N+1
          IF(N.GT.98)GO TO 7373
        IF(R.GT.EXNEGL)GO TO 1616
 7373   CONTINUE
        WRITE(61,1001)N
 1001   FORMAT(1H ,I2)
 9999 CONTINUE
      STOP
      END
```

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