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# Ecological and L-system based simulations of trace fossils

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## Abstract

Trace fossils represent the preserved interactions of trace making organisms with their environment. The form of traces should result from complex interactions among the organism's morphology, the behavior being carried out, the organism's perception of the environment, and the heterogeneity of the environment. Existing mathematical models for the biological formation of traces have tended to focus on a limited repertoire of behaviors, such as grazing. They do not include realistic patterns of environmental heterogeneity, differences in perception, or multiple behavioral responses. In addition, there have been almost no attempts to model 3-D traces, or traces that branch or anastomose. New models for grazing and crawling traces can be built on current research by ecologists into animal movement patterns and their interaction with environmental heterogeneity. These models explore the interactions of alternative spatial patterns of environmental heterogeneity with different perceptions and behavioral responses to it. They have the potential for suggesting how behavioral patterns for a given trace making organism might change as a function of environmental differences, such as resource distribution. This could be a useful tool for determining such patterns of spatial heterogeneity in ancient environments. A second approach can be based on recent developments in the computer-based study of morphogenesis. This technique utilizes L-systems and related methods for the generation of branching and 3-D theoretical morphologies. L-system descriptions can be quite complex and can incorporate realistic concepts of growth, including external environmental factors and signal transmission. They have been used previously for the production of simulated plants of startling realism. By altering the parameters used to generate the simulated fossils, a theoretical morphospace for trace morphology could be constructed.

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## 1. Introduction

With a few notable exceptions, progress in the numeric modeling and description of invertebrate trace fossil formation and distribution has noticeably lagged behind that of body fossils. A scatter-

ing of studies have attempted to simulate the behavioral processes responsible for the formation of trace fossils. Even fewer have attempted to quantify their spatial distribution. In this paper I will discuss some new numeric models for the generation of 2-D and 3-D trace fossils; these simulations will be based on ecological theories of animal movement in heterogeneous environments and on computer graphic models for morphogenesis.

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### 1.1. Existing models for trace fossil generation

As pointed out succinctly by Bromley (1990, p. 166), ‘above all, trace fossils are the tangible evidence of the behaviour of animals...’. Previous models for trace fossil generation have focused on how simple behavior patterns could produce observed trace morphologies. These models have also tended to focus on such morphologically complex and organized ichnogenera as *Helminthoidea* and *Spirorhaphe*.

The conceptual model of Richter (1924, cited in Papentin, 1973) forms the basis of most of these models. The underlying assumption of Richter’s scheme is that natural selection will tend to favor organisms that seek to maximize the area they cover relative to their path length (McGhee, 1998). As pointed out by Kitchell (1979), this optimization assumption is presumed to hold for organisms in food-limited environments. Richter proposed a horizontally burrowing organism that:

- moves a certain distance and then turns 180° (strophotaxis);
- stays close to previous tracks (thigmotaxis);
- avoids crossing previous tracks (phobotaxis).

These rules, with some modifications, were used by Raup and Seilacher (1969) to produce the earliest computer model of trace fossil movement. These modifications involved allowing the angle of strophotaxis to change, changing the distance between turns, and modifying the relative strengths of thigmotaxis and phobotaxis. Raup and Seilacher were able to successfully reproduce stereotypically meandering foraging trails. As pointed out by Prescott and Ibbotson (1996), this work stands as one of the earliest examples of research into what is now called artificial life or A-life (Ray, 1994; Adami, 1998).

Papentin (1973; Papentin and Röder, 1975) used a form of genetic algorithm to produce trace fossil movement patterns that ‘evolve’. Genetic algorithms are a method for approaching the optimal solution to a programming problem by estimating the fits of initial sets of parameters to the desired solution and then allowing the parameter sets to undergo processes akin to mutation, recombination and selection (Gershenfeld, 1999).

Only those sets with the highest fitness survive and reproduce. Papentin’s six parameters were based on those of Raup and Seilacher (1969) and included:

- the number of steps between spontaneous turns;
- turning when encountering a former track;
- avoiding paths between former tracks;
- keeping contact with former tracks;
- making an initial turn;
- switching between spiraling and meandering behavior after a certain number of steps.

His ‘worms’ could only make 90° turns. The fitness criterion of the model was the extent to which path crossing occurred; individuals (actually, solutions) which produced the fewest path crossings survived and reproduced.

Papentin had two initial parameter sets; one that would only go straight ahead and one that would turn randomly after each step. Remarkably, both initial sets evolved into virtual organisms that demonstrated strong phototaxis and thigmotaxis, although a number of alternative meandering and spiraling behaviors emerged.

More recently, Prescott and Ibbotson (1996) developed a robot model (using Legos!) that attempted to recreate the behavior of trace-forming organisms. The robot used a light sensor to detect a trail of paper that it deposits as it moves. They then programmed the robot with dominant phototactic behavior, weaker thigmotactic behavior, and a behavior that drove the robot forward when both thigmotaxis and phobotaxis were weak. This robot control architecture was able to produce simple spiraling traces. Slightly more complex architectures produced meandering traces. Prescott and Ibbotson suggested that the intelligence level exhibited by modern robot control systems is comparable to that of Vendian–Early Cambrian trace makers (Crimes and Fedonkin, 1994).

Hammer (1998) also used artificial life methods to simulate trace fossil evolution. He placed artificial organisms in a simulated world with areas of low and high nutrient content. The organisms have control systems that can evolve, with the fitness criterion being the amount of food ingested during their lifetime. Although there was a gener-

al trend to more efficient grazing patterns, Hammer was deeply pessimistic about how his results could be applied to real organisms, suggesting that any similarities in the form of real and simulated traces should be thought of as coincidental.

A different approach to the generation of traces was used by Kitchell (1979). She generated random movement pathways as null models to compare with observed deep-sea traces. She then used a variety of measures to determine the extent to which the observed traces were random or non-random. Kitchell also incorporated foraging theory into her analysis (see below).

A random walk model was also used by Hofmann (1990). He compared random traces to those of the trace fossil *Gordia*.

Garlick and Miller (1993) presented a simple computer movement program to model the geometry of foraging traces and some graphoglyptids. A more elaborate version of the program was used to model *Paleodictyon*, under the assumption that the trace represents a burrow by a single organism. It required that the trace making organism had the ability to measure angles and distances with considerable accuracy.

As pointed out by Crist and Wiens (1995, p. 733), ‘the ways in which animals move depend on their body size, vagility, and their responses to resource distributions and habitat structures’. With the notable exception of Kitchell (1979), previous models for trace fossil generation have not incorporated variability in resource distribution, other aspects of habitat heterogeneity, or concepts from foraging ecology. Existing models generally presume that the environment, at least locally, is homogeneous, with the exception of the presence of previous traces.

Existing models are also behaviorally simple and stereotypical. They represent only grazing behavior and do not incorporate differences among organisms in how they perceive their environment or alterations in behavior for a single organism as environments change (Miller and Curran, 2001). They also do not reflect multiple behaviors by the same organism, which may produce morphologically complex traces (Miller, 1998).

Finally, all existing trace fossil models are 2-D and thus essentially horizontal. There are no mod-

els that produce 3-D structures. Models have also not been developed for branching and cumulative structures such as *Chondrites* or boxworks such as *Thalassinoides*.

## 2. Foraging ecology and habitat heterogeneity

As described by Brown (2000), foraging ecology is concerned with the ecology and evolution of feeding behaviors by organisms. It is part of the larger discipline of optimal foraging theory, which also includes behavioral mechanisms and their controls and social aspects of foraging. A number of concepts from foraging ecology (Brown, 2000) have direct implications for the study of trace fossils:

- heterogeneity, both spatial and temporal, favors flexible feeding behaviors;
- there are behavioral tradeoffs between food acquisition and risk from predation;
- foragers respond to the spatial distribution of resources and their concentration, i.e. to the patchiness of resource distribution;
- spatial and temporal heterogeneity directly effects the coexistence of species.

Landscape ecology, in turn, is directly concerned with the nature and origins of this heterogeneity. An ecological landscape, according to the simple definition given by Turner (1989), is a spatially heterogeneous area. In this context, many geologic patterns, including the spatial distribution of trace fossils and ichnofabrics, can be viewed as landscapes in which there is a heterogeneous distribution of some property over a spatial extent.

The terminology used for landscape description is reviewed in detail in Forman (1995). Landscapes are heterogeneous mosaics of discrete, diagnosable, repeatable and generally homogeneous units. These basic units are landscape elements. Landscapes consist of a matrix, patches, and corridors. The matrix is the most extensive and continuous landscape element. Patches are smaller aggregates of landscape elements that are different from, and embedded within, the matrix. Patches can be of any size or shape. In this context, an individual trace could constitute a patch, which would be embedded in the sedimentary matrix.

Corridors are linear features that differ from the surrounding matrix, such as roads or power line cuts. In ichnofabric studies, a geometric analogue would be bedding planes.

The goals of landscape ecology include the description of landscape heterogeneity, the development of models to explain the origins of that heterogeneity, and determining the effects that this heterogeneity has on ecological processes (Turner, 1989). As a result, one major research area for landscape ecologists has been the effect of spatial heterogeneity on the movement of organisms. As pointed out by With (1994, p. 26): ‘Animal movement patterns are ideal for assessing species’ responses to heterogeneity because they provide a spatial record that documents how and at what scale(s) an organism responds to patch structure’. This strongly suggests that ecological studies into animal movement patterns would provide tremendous insights into the processes that affect fossil trace makers.

Animal movements have been studied by both simulation studies and by empirical studies using a variety of taxa (Bovet and Benhamou, 1988; Turchin, 1998; Ritchie, 1998; Erlandsson et al., 1999; Farnsworth and Beecham, 1999; Wu et al., 2000). With (1994) examined the movement patterns of three species of grasshoppers across a grassland mosaic. Her goal was to determine how differences in an organism’s grain (the finest resolution at which it perceives heterogeneity) and extent (largest scale at which an organism senses its environment) affects its movement patterns. Using fractal analysis, she determined that the smaller species moved in a more tortuous pattern than the larger species, suggesting that their perceptions of the landscape are different. With suggested that fractal analysis can thus be a tool for assessing an animal’s grain and extent.

Crist and Wiens (1995) conducted field and simulation studies of beetle movements in a semi-arid grassland, with the goal of determining how movement patterns influenced rates of capture in pitfall traps. Among the field techniques used was to map the path that an individual beetle took by marking its location every 5 s. They then measured parameters such as distances moved per time step and turning angles between steps. Two

different sets of movement rules were used in the simulations. The first set used random draws from the empirical distributions of turning angles and movement distances. The second set used correlated random walks, where the variables were the distance moved per time step, the variance in the distance moved, and the turning angles.

A variant of a random walk model was also used by Gustafson and Gardner (1996) in a study of dispersal between separated patches of preferred habitat (e.g. fragmented forest patches). They began with a digital land-cover map, consisting of gridded cells belonging to different habitats and with one type of habitat being preferred by the model organism. Each habitat type was assigned a probability that an organism would enter it, with the degree of heterogeneity in the landscape controlled by adjusting the relative probabilities. Beginning at a patch of preferred habitat, the organism then random walked across the landscape, with the provision that the organism could not re-enter a grid cell that it just left (a self-avoiding random walk), until it encountered another patch of the preferred type.

Schippers et al. (1996) also used a grid-based random walk model to simulate the movement of badgers in Holland. Probability of movement from one cell to another was presumed to be a function of the relative preference for a particular habitat type, whereas movements within preferred habitat types were random, with some dependence on previous directions of movement.

Both simulations and field data were used by With et al. (1999) to examine the ability of organisms to disperse across landscapes with different patterns of spatial heterogeneity, expressed as the abundance and distribution of preferred habitat types. Their ‘cybercrickets’ moved through these landscapes, depending on different rules for perceiving preferred habitat.

In one of the very few studies of benthic marine organisms, Erlandsson et al. (1999) examined the movement of the intertidal rocky shore dwelling limpet *Cellana grata*. They mapped the path of limpet movement, measured characteristics such as trail length and tortuosity, and compared the trail to the measured complexity of the rock surface. They determined that actual trail length was

much greater than net displacement, reflecting the complexity of the path, and that the trail became more tortuous as surface roughness increased.

Finally, [Ritchie \(1998\)](#) directly tied together foraging ecology and landscape ecology in a model for foraging in a fractal environment. He examined the interrelationships among the distribution of favorable habitats, the distribution of resources among these habitats, and the ‘foraging scale’ of the organisms (scale at which an organism perceives the landscape). Different patterns of habitat and resource distribution favor different foraging scales and different degrees of resource specialization. A recent study by [Chase et al. \(2001\)](#) of freshwater snails lends support to these concepts.

These studies suggest elements that models of crawling, grazing, and feeding traces should incorporate:

- Spatial heterogeneity of the substrate, such as resource distribution or firmness, preferably at multiple scales;
- Preferences of the moving organism for some aspect or aspects of the environment, such as a particular resource or set of resources;
- Variations among organisms in their perception of this variability and their behavioral response to it, including the ability for an individual organism to change its behavior;
- Alteration of the environment caused by the movement of the organism through it;
- Energetic costs and consequences of different movement patterns in the presence of heterogeneity;
- Inter- and intraspecific competition.

[Kitchell \(1979\)](#) is the only study of which I am aware that has incorporated foraging theory concepts into the study of traces. She examined the hypothesis, based on optimal foraging theory, that foraging traces produced in non-food limited areas, such as the shallow shelf, should be random, whereas traces in the food-limited deep-sea should be non-random. She examined numerous photographed traces from the Arctic and Antarctic and used various measures to determine whether they were random. Kitchell’s results indicated that although the observed traces were not random, there was no significant relationship between trace morphology and depth. She sug-

gested that patchiness of resources, as well as competition and predation avoidance, may play a role in structuring traces.

### 3. Foraging simulations

As a starting point in examining how models that incorporate some of these concepts can be applied to the study of trace fossils, I have developed a simple simulation of how a surface deposit feeder might move across a heterogeneous seafloor. This model is derived from the cellular automata landscape dispersal program CAPS described by [Plotnick and Gardner \(2002\)](#). The basic assumption of the model is that an organism will move toward the greatest local abundance of resources, with nearby resources being preferred to those more distant.

#### 3.1. Modeling the landscape

Spatial heterogeneity was modeled using site specific variability in resource concentration. Two patterns of spatial heterogeneity were used. In the first, a resource was randomly distributed across a  $128 \times 128$  grid ([Fig. 1](#)). The amount of resource in each grid cell is represented by a random real number chosen from a uniform distribution from zero to one.

In the second, I used a fractal generating algorithm to generate a fractal, and thus clustered, resource distribution over the same grid size ([Fig. 2](#)). Fractal maps are produced using a version of the midpoint displacement algorithm of [Saupe \(1988\)](#). Maps are characterized by a parameter  $H$  that ranges from zero to one ([Plotnick and Gardner, 2002](#)); low values of  $H$  (near zero) produce maps that are extremely fragmented, whereas  $H$  values near one produce highly aggregated maps. The aggregated map in [Fig. 2](#) was produced using an  $H$  value of 0.7. The range of resource values is again a series of real numbers varying between zero and one.

#### 3.2. Modeling perception and movement

Animal movement in these landscapes is a func-

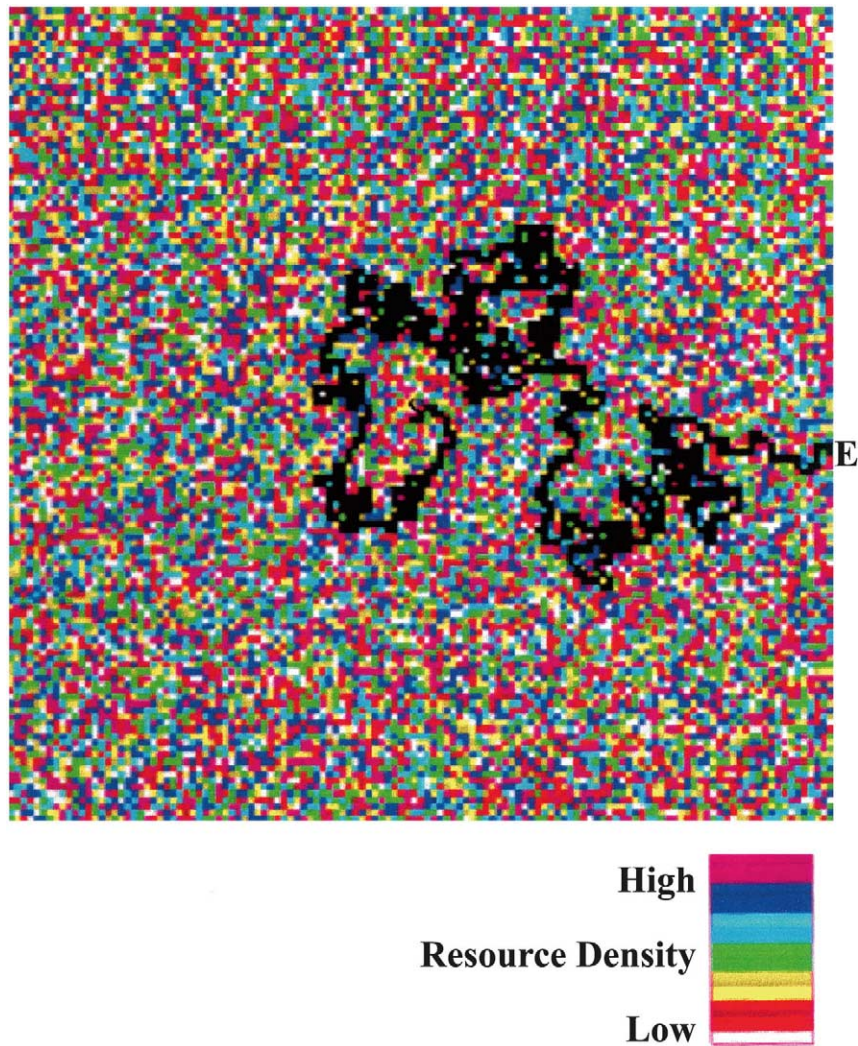


Fig. 1. Movement of a simulated organism across a random resource landscape. The landscape consists of a series of real numbers between 0 and 1, with resource level shown by the colors. The black pixels indicate the path from the center towards the edge of a 'cyberworm' that moves toward local areas of higher resource concentration. E marks the end point of the run.

tion of resource concentration and distance. As a starting point, I used the following behavioral rules for a 'cyberworm':

- eat all the food in the cell you are in;
- examine the four horizontally and vertically adjacent cells (the nearest neighbor cells or von Neumann neighborhood (Plotnick and Gardner, 1993)) and move to the cell with the highest resource;
- if the four nearest neighbor cells have no food, then move to the nearest diagonal cell (the

next nearest neighbor or Moore neighborhood) with the highest food resource;

- if none of the eight nearest cells have food, then move randomly until you encounter a cell that does.

Because the organism does not move to cells where food has already been exhausted, it minimizes the number of possible path recrossings.

The organism is initially placed at the center of the grid. The simulation terminates when it reaches the edge.

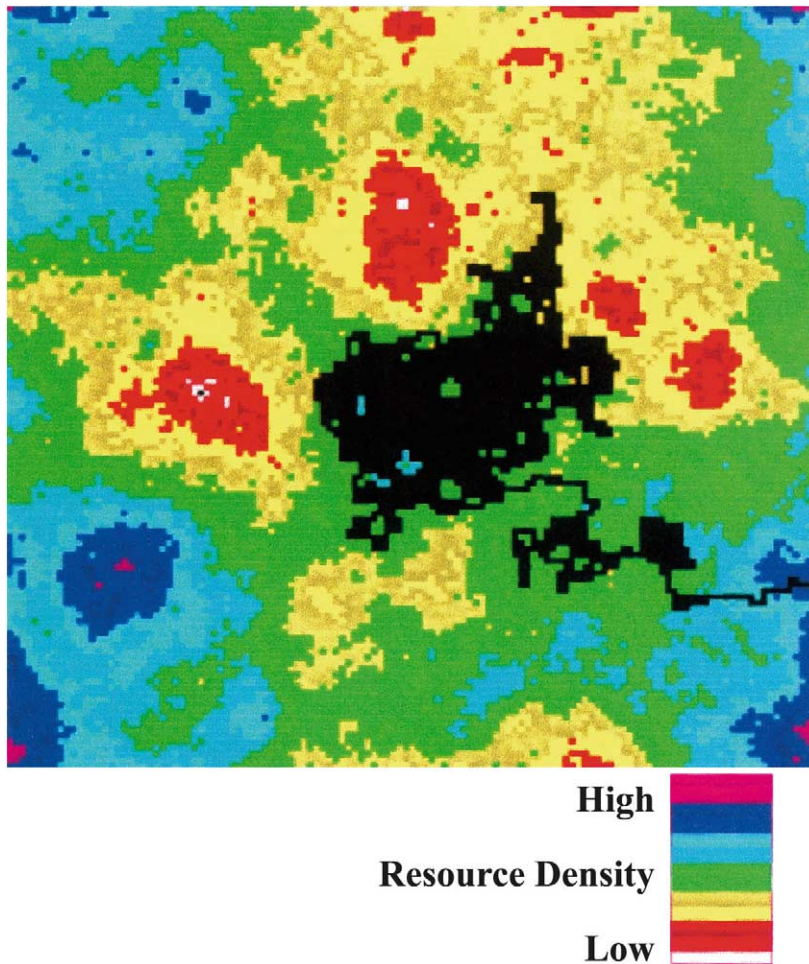


Fig. 2. Movement of a simulated organism across a fractal resource landscape. Resource range is the same as in Fig. 1; the fractal pattern produces a clustered distribution of resources. The path of the simulated organism (black pixels) moves up resource gradients and exploits areas of higher resource concentration.

The paths in Figs. 1 and 2 show the results of one realization in each of the two environments. A number of differences are visible. For example, although both trails contain linear segments, the trail in the fractal environment includes a compact area that originally contained a large resource concentration. Note also that the organism in the fractal environment moves up a resource gradient (lower right edge).

This model, along with all previously developed trace fossil models, is an ‘individual based movement model’ or IBMM (Turchin, 1998). These models are Lagrangian, in that they focus on

the moving individual rather than a point in space, and contain a mix of both deterministic and stochastic components (Turchin, 1998).

This model is also closely related to various ‘agent’ models, such as Swarm, that have been developed over the past decade (Minar et al., 1996) and have found wide usage in simulating social and economic systems. Agents are simulated entities in a system that possess at least some degree of autonomy and take actions that potentially affect themselves and other agents. Most of such models contain multiple interacting agents.

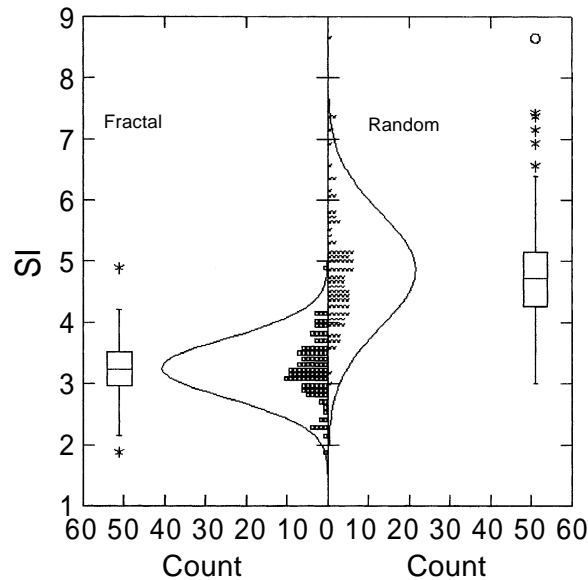


Fig. 3. Comparison, using the Shape Index (SI) of Patton (1975) of movement paths in 100 each simulated movement paths in simulated fractal and random landscapes. SI measures the ratio of interior to edge in the paths. The paths in the random landscapes are significantly more elongated than those in the fractal landscapes, a reflection of the spatial concentration of resources in the latter.

### 3.3. Comparing movement patterns

The difference between the two movement paths was characterized using the Shape Index (SI) of Patton (1975). If  $P$  is the perimeter for the path and  $A$  is the path area, then  $SI = 0.25 * P / \sqrt{A}$ . For a square,  $SI = 1$ ; the more elongate the path, the greater the value of SI.

One hundred runs on each map type were simulated. Fig. 3 compares the frequency distributions of the SI values; based on a  $t$ -test, they are significantly different at  $P < 0.001$ . Movement in random landscapes is thus more linear and less compact than in fractal landscapes. This is not surprising, given the spatial concentration of resources in fractal landscape. This analysis suggests that the form of foraging traces could be a useful tool for determining such patterns of spatial heterogeneity in ancient environments.

### 3.4. 3-D movements

The model can readily be expanded to three dimensions. Fig. 4 shows a simulated movement

pattern in a 3-D resource space. This space was generated producing a  $50 \times 50 \times 50$  array of real random numbers ranging from zero to one. A depth gradient was then added by decreasing the amount of resource in each cell by the value 0.02 for each increment of depth. For ease of computing, movement was constrained only to the four cardinal directions and up or down. A more realistic version of this should also incorporate realistic changes in physical and chemical properties with depth.

### 3.5. Discussion

The model can obviously be made more complex. For example, organisms are probably sensitive to the overall strength of a signal (i.e. a water born chemical), which is a function of both concentration and distance, rather than distance or concentration individually. In this case, it will be necessary to use algorithms that incorporate the decay of a signal as a function of distance, similar to those used for dispersal in the CAPS model (Plotnick and Gardner, 2002).



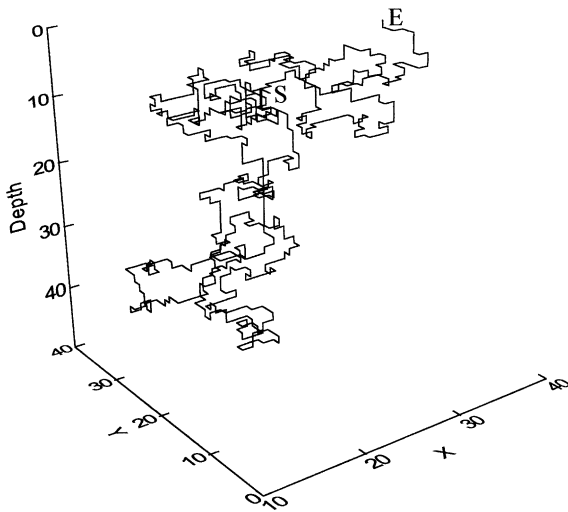


Fig. 4. Representative movement path in a 3-D random resource volume, with a depth gradient. Resource concentrations are random, with a superimposed increasing trend towards the top. S indicates the starting point and E the ending point of the run.

Alternatively, organisms do not live in isolation; both inter- and intraspecific competitors for resources might exist, as well as predators (Kitchell, 1979). Current ideas in foraging (Brown, 2000) strongly suggest that predation plays a major role in modifying the response of organisms to available resources. Introducing biotic interactions allows the option of using genetic algorithms similar to those of Papentin (1973) and Hammer (1998) to computationally evolve superior trace makers, as well as the rich resources developed for agent simulations. It might then be possible to devise a ‘theoretical design space’ (Hickman, 1993), where the axes are behavioral rather than morphological.

A final improvement would be to allow the replenishment of resources at some time following their initial removal. This could also be linked with models that incorporate sedimentation. The model should also be modified to include the energetic costs of movement and resource acquisition, as well as multiple resources.

#### 4. L-system models

Despite their importance in the record, with the

exception of the model of *Paleodictyon* described by Garlick and Miller (1993), I am aware of no attempts to model 3-D, branching, interconnecting, or cumulative ichnotaxa. As discussed by McGhee (1998), numerous methods now exist to produce theoretical morphospaces for branching organisms, such as trees or bryozoans. In this section I would like to suggest that one of these methods, Lindenmayer systems (L-systems), are especially promising for the modeling of trace fossil morphogenesis in biologically realistic ways.

L-systems were originally developed by Aristid Lindenmayer for the modeling of the development of multicellular organisms, such as plants (Prusinkiewicz and Lindenmayer, 1990). They have since been developed and refined and used to produce graphical simulations of plants and other organisms of incredible realism (Prusinkiewicz and Lindenmayer, 1990; Jacob, 1995).

L-systems are a form of *rewriting system*, where the parts of a simple object are successively replaced using a specific set of rules. These are usually expressed as a set of character strings, where the rule specifies that a particular character in the string is to be replaced with another character or set of characters. For example, assume an alphabet consisting of the characters A and B. We will specify the rewriting rules (known as *productions*) that the letter A is to be replaced by the letters AB and the letter B by the letter A. Starting with the initial letter B (the *axiom*) the following strings result: B; A; AB; ABA; ABAAB, etc.

The L-system approach can be used to draw objects by using strings that specify how to move the cursor on the screen. Known as turtle graphics, based on a comparison to a robot turtle drawing a line, they include symbols such as:

- F: move forward a fixed distance and draw a line;
- +: turn right by a specified angle;
- -: turn left by a specified angle.

The reference frame for the movements is the current orientation of the ‘turtle’, rather than an external one.

For example, if the angle is 90°, the string F+F+F+F draws a box. The L-system specifies how each element of the string should be rewritten at successive iterations. For example, if the

initial string or axiom is +F (turn 90° and move forward) and the rewriting rule is ‘replace F by F–F+F’, then the successive strings would be: +F; +F–F+F, +F–F+F–F–F+F+F–F+F, etc.

Branching in L-systems is produced by using the symbols [ and ]. The former essentially says ‘remember where you are and your orientation’, whereas the latter indicates ‘go back to where you were’. The string F[+F]F would thus mean: ‘go forward, remember where you are and your orientation, turn right and move forward, go back to the orientation and position you remember, go forward’. The result would be a straight line with another line coming off at an angle. Additional symbols indicate turns in space and thus allow 3-D branching systems.

An alternative way to describe L-system graphics is that one part of a geometric figure is replaced by another geometric figure, with the replacement occurring iteratively. For example, in Fig. 5, the original solid line (Fig. 5A) is the axiom. The rewriting rule replaces it by a hollow line and two solid lines at a 120° angle (Fig. 5B). At the next iteration, the two solid lines are in turn replaced. This is equivalent to the simple growth rule: ‘branch and grow forward’ or in L-system grammar:  $F \rightarrow [+F][-F]$ , where the angle of the turn is 60°.

A simple modification of this rule would be  $+F[\wedge(90)F][+F][-F]$ , where  $\wedge(90)F$  means ‘erect a vertical branch at 90° at each branch point’. Fig. 6 illustrates five iterations of this rule. The pattern produced is very similar to that of the enigmatic trace fossil *Paleodictyon* (Seilacher,

1977; Garlick and Miller, 1993; Levin, 1994; Wetzel, 2000). I have observed similar ‘dangling ends’; i.e. the unattached ends, in specimens of this fossil from the Eocene of the Carpathians. Seilacher (1977) also illustrated numerous incomplete meshes.

This model produces vents at every vertex. A simple modification, illustrated in Fig. 7, can also produce vents at the middle of a side. Seilacher (1977, fig. 14) illustrates both types of vent patterns. The L-system thus provides a simple model for how this highly organized trace could be produced, as well as variations in morphology. Based on this model, I would predict that the trace forming organism is a modular form that propagates by branching, rather than a burrower. If true, *Paleodictyon* is a consequence of growth rather than behavior.

L-systems also allow the simulation of 3-D morphologies. The image in Fig. 8 represents a simple graphical model of a *Chondrites*-like trace. It is based on similar models for the production of branching plant morphologies (Prusinkiewicz and Lindenmayer, 1990) and was produced by iteratively branching a structure at a fixed range of angles, with the addition of some randomness. By changing the number of branches produced at each iteration, the angle between the branches, and the length of the branches a ‘*Chondrites* morphospace’ could be produced for comparison with real fossils (Ekdale, 1992; Savdra, 1992).

L-system descriptions can be quite complex and can incorporate realistic concepts of growth, including sensitivity to external environmental fac-

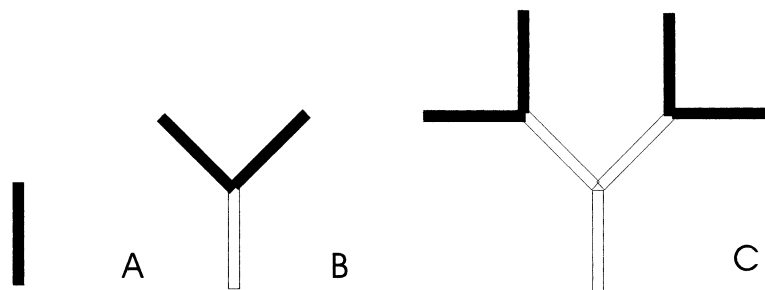


Fig. 5. Simple L-system representation of repetitive branching. The initial line or axiom (solid line in (A)) is replaced by the hollow line and two solid lines at 120° relative to each other (B). This is the rewriting rule or production. The rule can then be iteratively applied. The first iteration produces the pattern shown in (C).

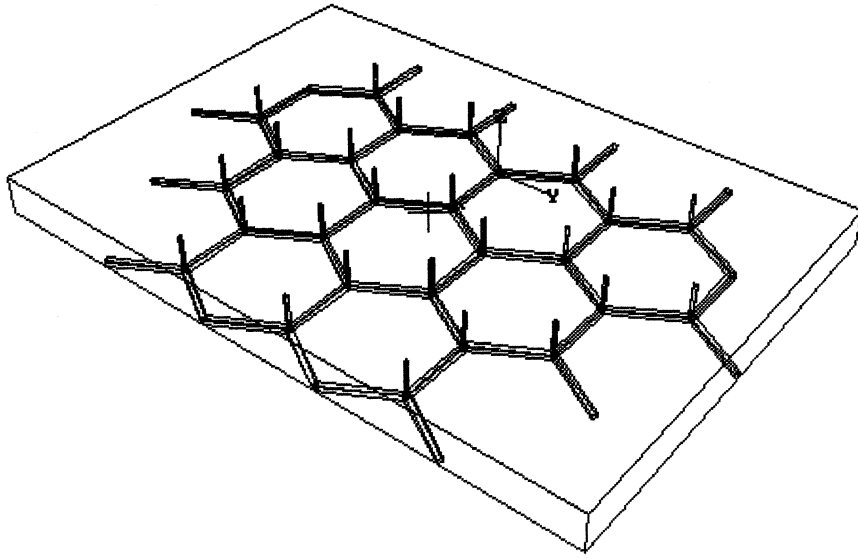


Fig. 6. Five iterations of the L-system shown in Fig. 5, with the addition of a vertical tube at each vertex. This can be compared with the illustration of *Paleodictyon* shown in Seilacher (1986, fig. 3–12 g).

tors and internal signal transmission (Prusinkiewicz and Lindenmayer, 1990; Berger, 1991; Morelli et al., 1991; Mech and Prusinkiewicz, 1996). L-systems can also be integrated with genetic algorithms to produce L-systems that evolve to meet given selection criteria (Jacob, 1995). There are

also available other possible models of morphogenesis, such as diffusion limited aggregation and Eden models, which may also be useful in trace fossil simulation (Plotnick and Gardner, 1993; Kaandorp, 1994).

Software for interpreting and drawing L-sys-

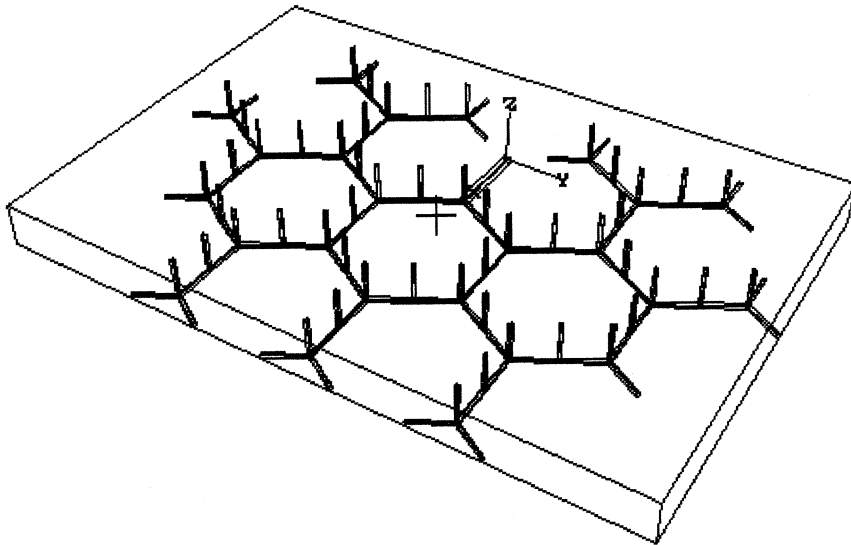


Fig. 7. Modification of the L-system in Fig. 6, producing a vertical tube at the midpoint of each side. Compare with Seilacher's (1986) fig. 3–12 h.

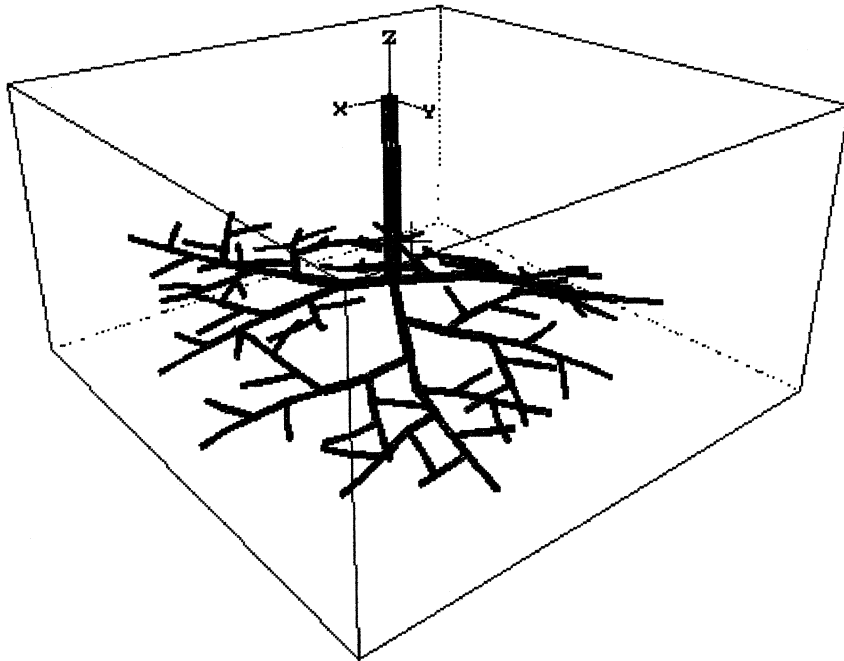


Fig. 8. L-system model of a *Chondrites*-like trace. Branches are produced at acute angles, with the addition of some randomness. Branch angles, length and number can be easily modified, allowing the production of a ‘*Chondrites* morphospace’.

tems is readily available online (see <http://www.xs4all.nl/~ljlapre/> or <http://www.cpsc.ucalgary.ca/Redirect/bmv/software.html>). The L-systems used in this paper were generated using the Lparser and Lviewer software written by Laurens Lapré (<http://www.xs4all.nl/~ljlapre/>).

## 5. Conclusions

An improved understanding of the controls of trace formation has the potential to improve our understanding of the long-term evolution of animal behavior. Phanerozoic changes in the nature of ichofabrics are well documented (Bottjer and Droser, 1994), as are changes in the diversity and environmental distribution of ichnofossils (Crimes and Fedonkin, 1994; Orr, 2001).

The evolution of behavior as documented by trace fossils is more controversial. Seilacher (1986 and elsewhere) argued that various groups of deep-sea trace fossils show a long term trend towards ‘optimization’, where optimization is

measured by the completeness of coverage of an area by the trace. Therefore, optimal foraging traces have features such as tight turns and close packing of meander loops. Crimes and Fedonkin (1994), in contrast, found no evidence of an optimization during the Phanerozoic in trace fossil morphology, with the possible exception of spiral traces. More recently, Wetzel (2000), based on the assumption that *Paleodictyon* represents a burrowing trace, used the existence of an extremely large Eocene form of this ichnogenus to argue against optimization.

As discussed above, this optimization argument, which Kitchell (1979) called the trace fossil paradigm, presumes the foragers live in a food-limited environment. Her examination of modern traces showed no relationship between food availability and trace morphology.

I would argue that what is needed is a new conception of what is meant by ‘optimal’ in the context of trace formation. The modeling results presented here suggest that trace form is at least as dependent on the patterns of environmental

heterogeneity as on behavioral programs. Any comparison of putative optimal morphologies with real traces needs a far more complete and nuanced concept of what optimal morphology should be for a given set of environmental conditions.

The L-system approach, in this context, gives an alternative way of specifying the minimum number of behavioral rules that are needed to generate a given trace form. They have the potential of determining how these rules might be altered in the context of evolution or environmental changes to produce alternative morphologies.

The last several decades have seen significant advances in our understanding of the behavioral, ecological, and sedimentological aspects of trace fossil formation and preservation. What has clearly been lacking, however, is integration of these concepts with the large and growing body of ecological literature that examines the movements of organisms and their relationship with environmental heterogeneity. The areas of landscape ecology and foraging ecology, as well as artificial life, have much to teach ichnologists.

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