Artificial Life & Complex Systems

Lecture 3

Patterns

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- Patterns
- Dynamical Systems
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- Pattern formation
- Morphogenesis

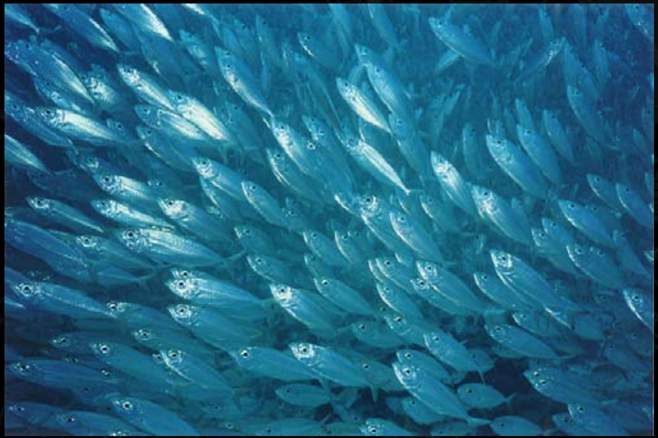
[Paper: A.M.Turing (1952) CLASSIC!]

What is a Pattern?

Pattern = organized arrangement of objects in space and time

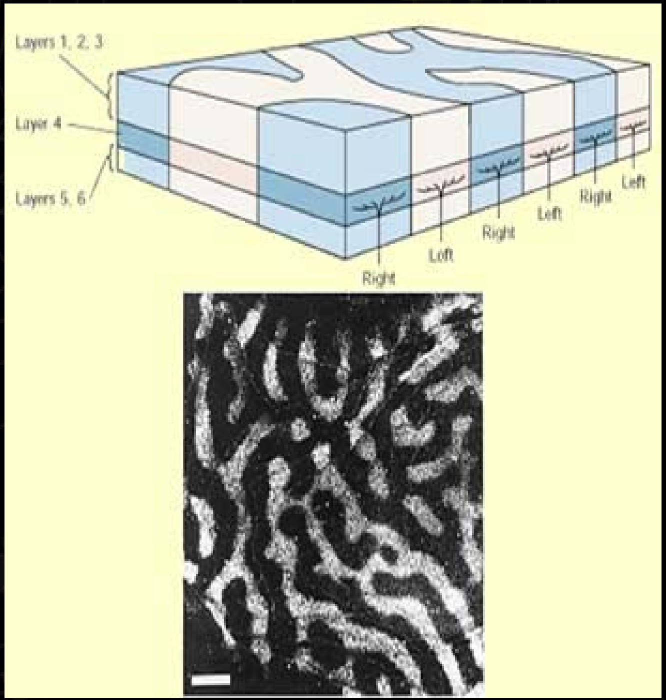
Examples of biological patterns:

- Schools of fish
- Raiding column of army ants
- Ocular dominance stripes in visual cortex
- Synchronous flashing of fireflies
- Pigmentation patterns on shells



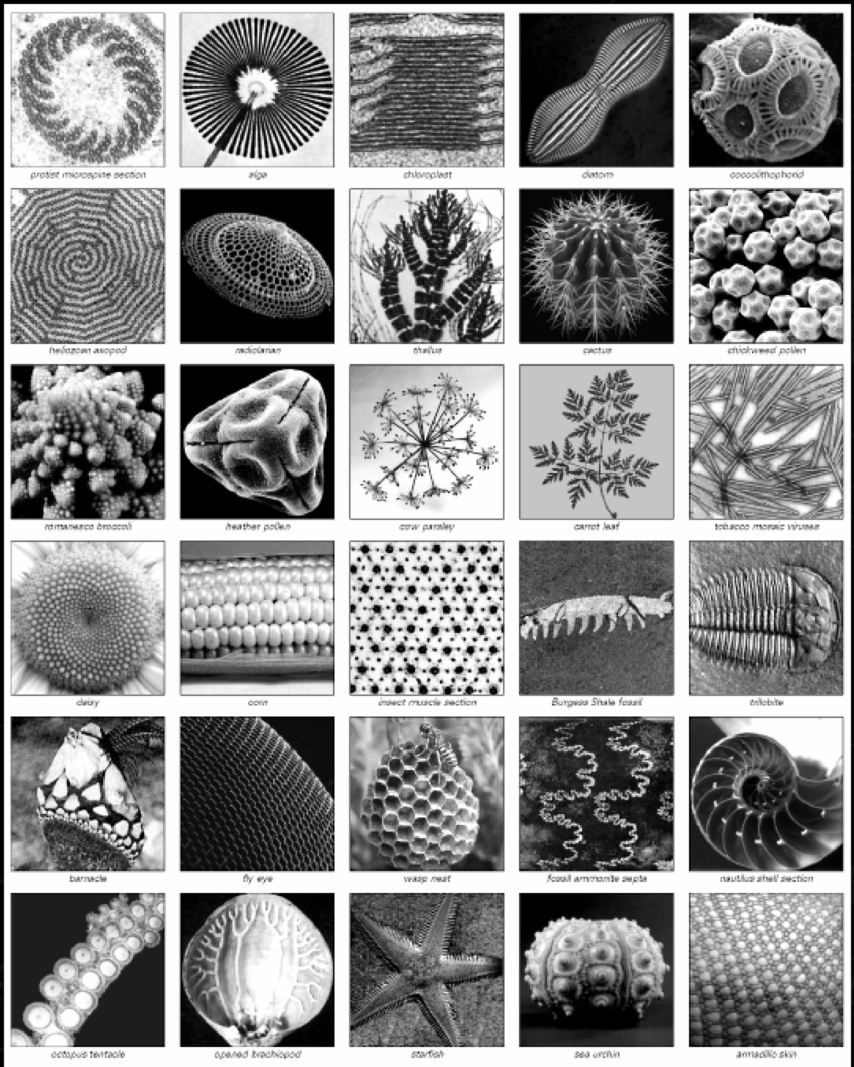
school of fish

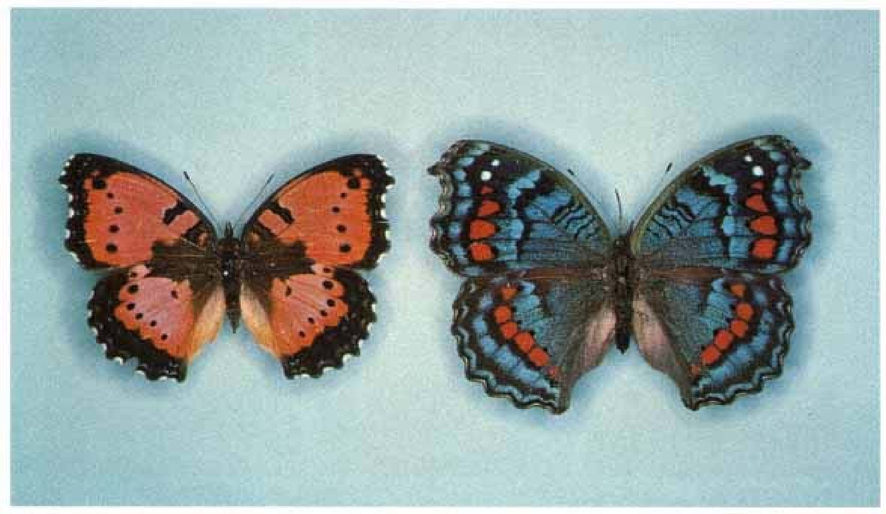
fireflies

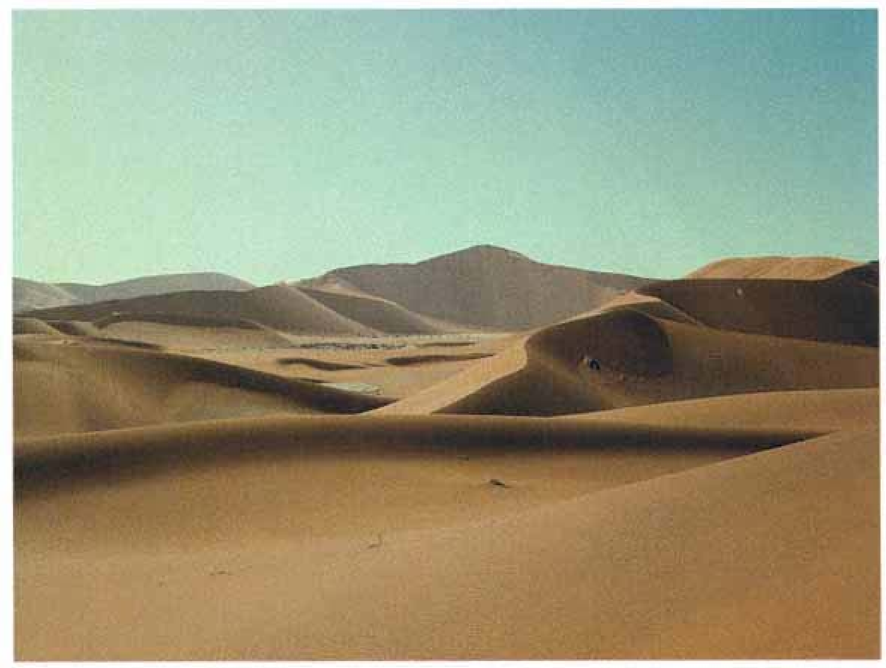


inputs from left eye (black) and right eye (white)

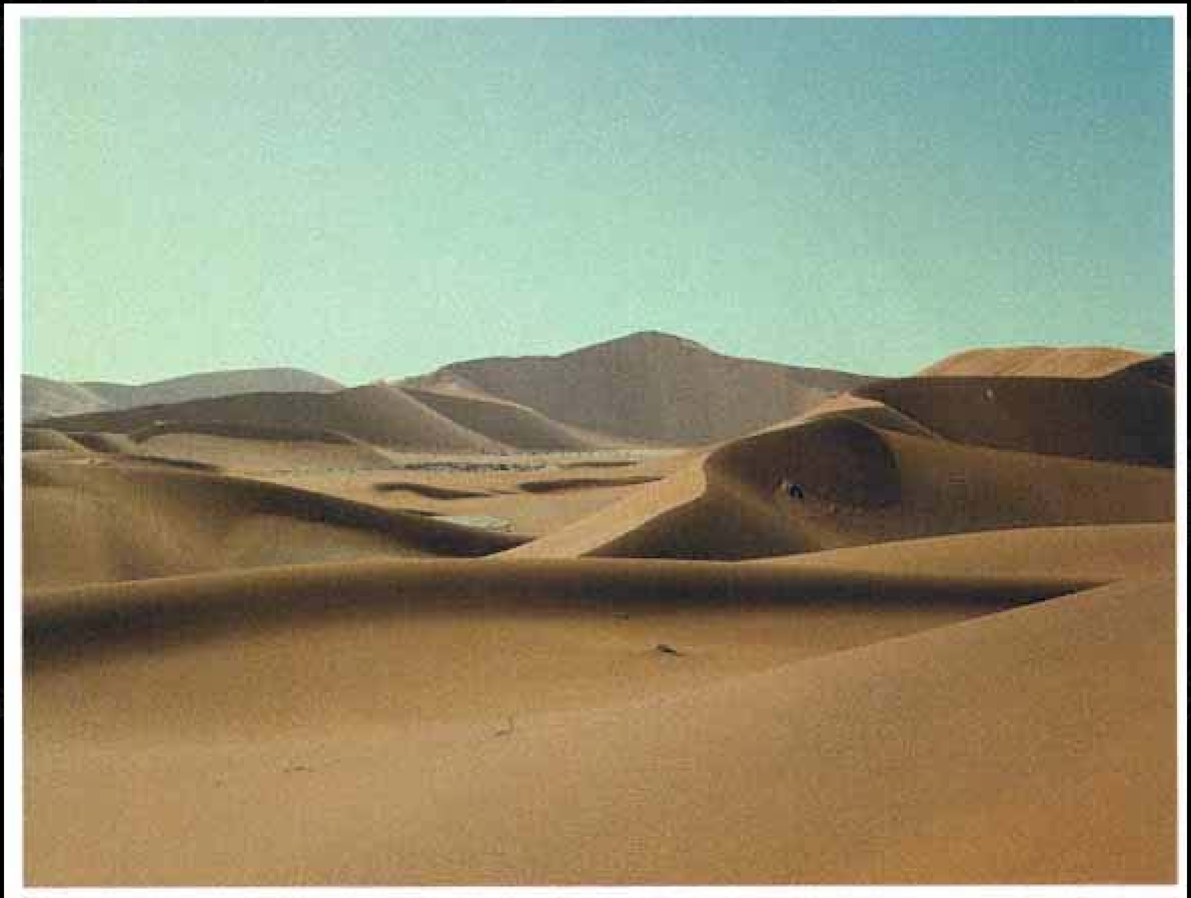
More Patterns







More Patterns

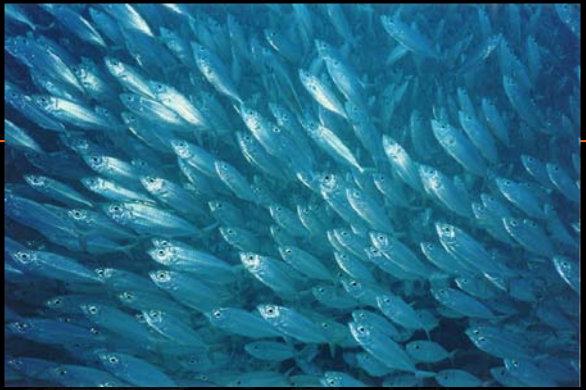


Pattern Formation

If Nature is at all economical (probably, yes), we can expect that she will choose to create complex form not by piece-to-piece construction by organizational and pattern-forming phenomena we see also in the non-living world.

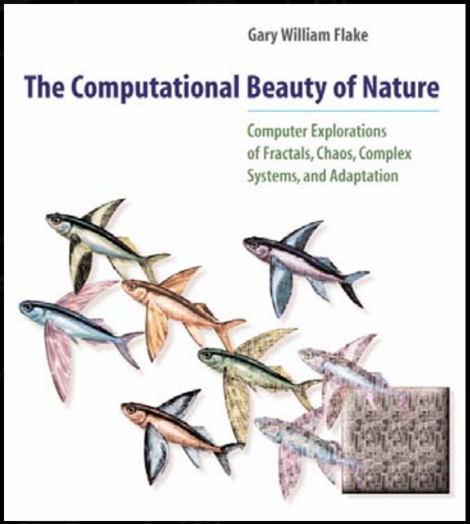
If this is true, then there must be similarities in the form and patterns of living and purely inorganic or physical systems.

How Does Nature Build Patterns?



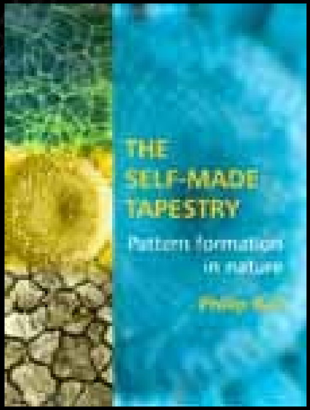
Buildings blocks are:

- Living units (fish, ants, nerve cells, …) → biological systems
- Inanimate objects (bits of dirt, sand, …) → physical/nonbiological systems



Differences between physical and biological systems:

- In biological systems the subunits are more complex
- The interactions among the subunits are influenced also by genetically controlled properties (in physical systems interactions are purely physical)



How Are Patterns Formed? Any Ideas?

How Are Patterns Formed?

Simple answer: “Form follows function”

That is, the shape and structure of a biological/technological system – a protein molecule, a limb, an organism, a colony, the Internet – is that which best equips the system for survival

A form which gives organism (system) an evolutionary advantage tends to stick

Power of cumulative selection

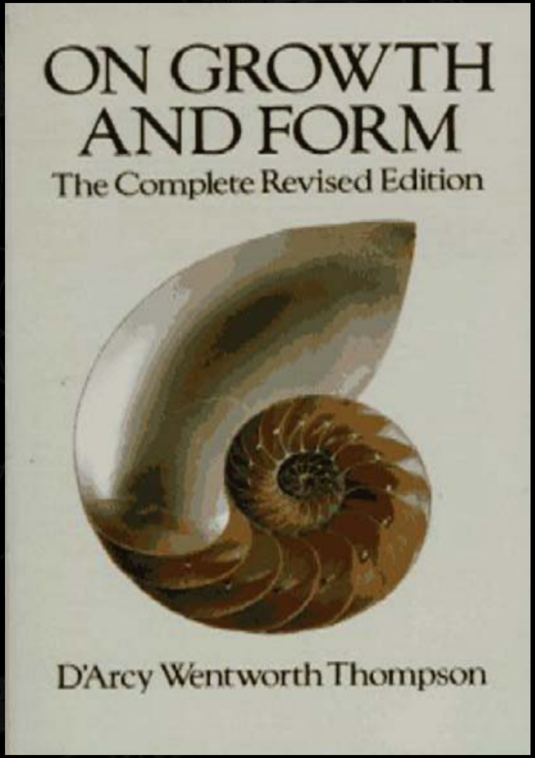
How Are Patterns Formed?

Natural selection is not entirely satisfying ... Why?

How Are Patterns Formed?

1) It says nothing about the underlying <u>mechanisms</u>!
2) Why should the pattern on a shell be of advantage?

Once you start to ask the ‘how?’ of mechanism, you are up against the rules of chemistry, physics, and mechanism, and the question becomes not just ‘is the form successful?’ but ‘is it physically possible?’



(1917)

How Are Patterns Formed?

Another simple answer: Emergence!

Patterns emerge from large populations of interacting ‘units’ (living organisms and non-living entities)

Emergence implies that the large-scale organization could never be deduced by close inspection of the individual units (holistic perspective, e.g. H_20)

How Are Patterns Formed?

Can simple rules give rise to patterns and forms?

Mechanisms

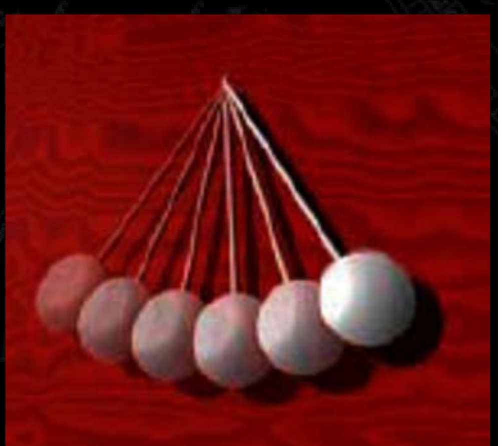
- Iteration
- Recursion
- Feedback

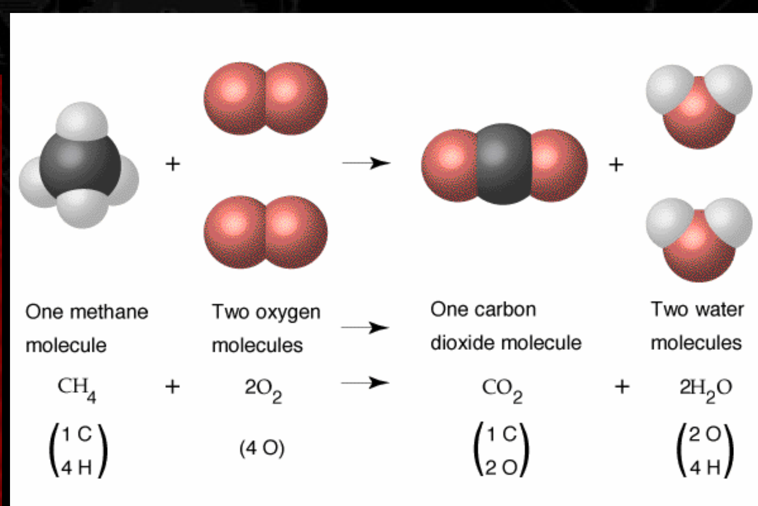
Can give rise to self-similar structures such as trees, plants, clouds, mountains, ...

What is a Dynamical System?

Characterization:

- A system that evolves in time according to a set of rules
- What changes in time is a variable (e.g. position, concentration, temperature, viscosity, ...)
- Present conditions determine the future.
- The rules are usually nonlinear (e.g. set of diff. eq. defining rates of change)
- There may be many interacting variables





$$\boxed{\{S_1, S_2, \cdots, S_n\}} \quad 1)$$

$$\boxed{\begin{aligned} \frac{dS_1}{dt} &= f_1(S_1, S_2, ..., S_n) \\ \frac{dS_2}{dt} &= f_2(S_1, S_2, ..., S_n) \\ &\cdots \\ \frac{dS_n}{dt} &= f_n(S_1, S_2, ..., S_n) \end{aligned}} \quad 2)$$

Dynamical Systems at a Glance

Figure 1.3.1

Number of variables →

Nonlinearity →

	$n = 1$	$n = 2$	$n \geq 3$	$n >> 1$	Continuum
	Growth, decay, or equilibrium	*Oscillations*		*Collective phenomena*	*Waves and patterns*
Linear	Exponential growth RC circuit Radioactive decay	Linear oscillator Mass and spring RLC circuit 2-body problem (Kepler, Newton)	Civil engineering, structures Electrical engineering	Coupled harmonic oscillators Solid-state physics Molecular dynamics Equilibrium statistical mechanics	Elasticity Wave equations Electromagnetism (Maxwell) Quantum mechanics (Schrödinger, Heisenberg, Dirac) Heat and diffusion Acoustics Viscous fluids
			Chaos	*The frontier*	*Spatio-temporal complexity*
Nonlinear	Fixed points Bifurcations Overdamped systems, relaxational dynamics Logistic equation for single species	Pendulum Anharmonic oscillators Limit cycles Biological oscillators (neurons, heart cells) Predator-prey cycles Nonlinear electronics (van der Pol, Josephson)	Strange attractors (Lorenz) 3-body problem (Poincaré) Chemical kinetics Iterated maps (Feigenbaum) Fractals (Mandelbrot) Forced nonlinear oscillators (Levinson, Smale) Practical uses of chaos Quantum chaos ?	Coupled nonlinear oscillators Lasers, nonlinear optics Nonequilibrium statistical mechanics Nonlinear solid-state physics (semiconductors) Josephson arrays Heart cell synchronization Neural networks Immune system Ecosystems Economics	Nonlinear waves (shocks, solitons) Plasmas Earthquakes General relativity (Einstein) Quantum field theory Reaction-diffusion, biological and chemical waves Fibrillation Epilepsy Turbulent fluids (Navier-Stokes) Life

Other Examples of (Nonlinear) Dynamical Systems

- The Solar System
- The atmosphere (the weather)
- The economy (stock market)
- The human body (heart, brain, lungs, ...)
- Ecology (plant and animal populations)
- Cancer growth
- Spread of epidemics
- Chemical reactions
- The electrical power grid
- The Internet

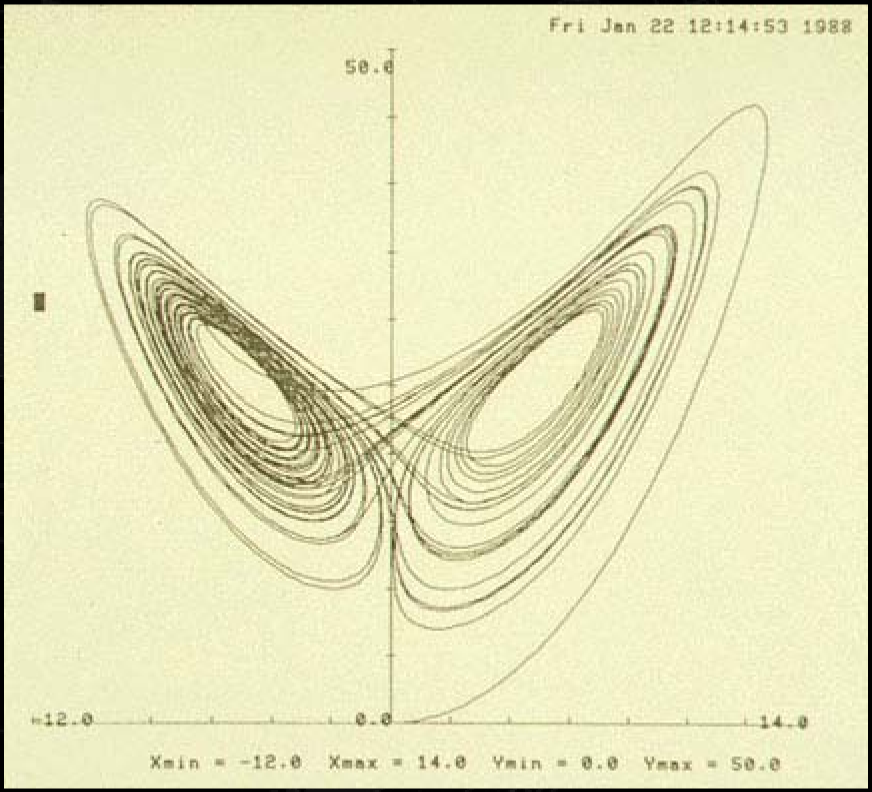
Phase or State-Space

Def.: Map of variables in time

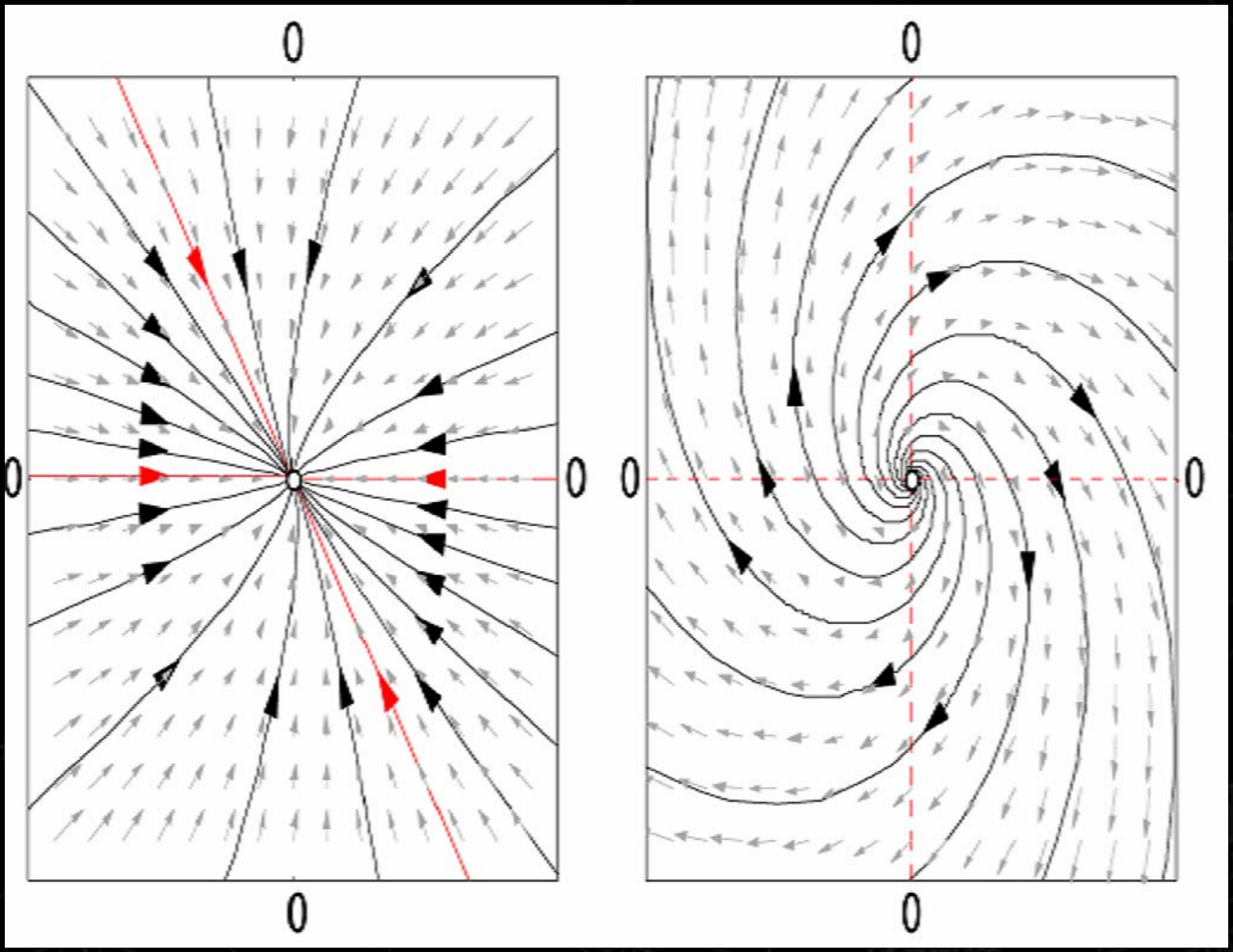
- Time is parameter
- Trajectory (orbit) in state space

E.g. $Z(t) = [x(t), x(t+1), x(t+2)]$

Interestingly, for <u>continuous (reversible) systems</u>: Only one trajectory passes through each point of a state-space (not true in discrete systems)



Vector Fields



DEMO:

Attractors

Phase-space volume to where dynamical system converges asymptotically over time

Why Attractor Behavior?

Energy dissipation (thermodynamic systems)

- Friction, thermodynamic loss, loss of material, etc.
- Volume contraction in phase-space (system tends to restrict itself to small basins of attraction)
- Self-organization (dissipative systems)

Compare with ...

Hamiltonian systems

- frictionless, no attractors
- Conservation of energy
- ergodicity

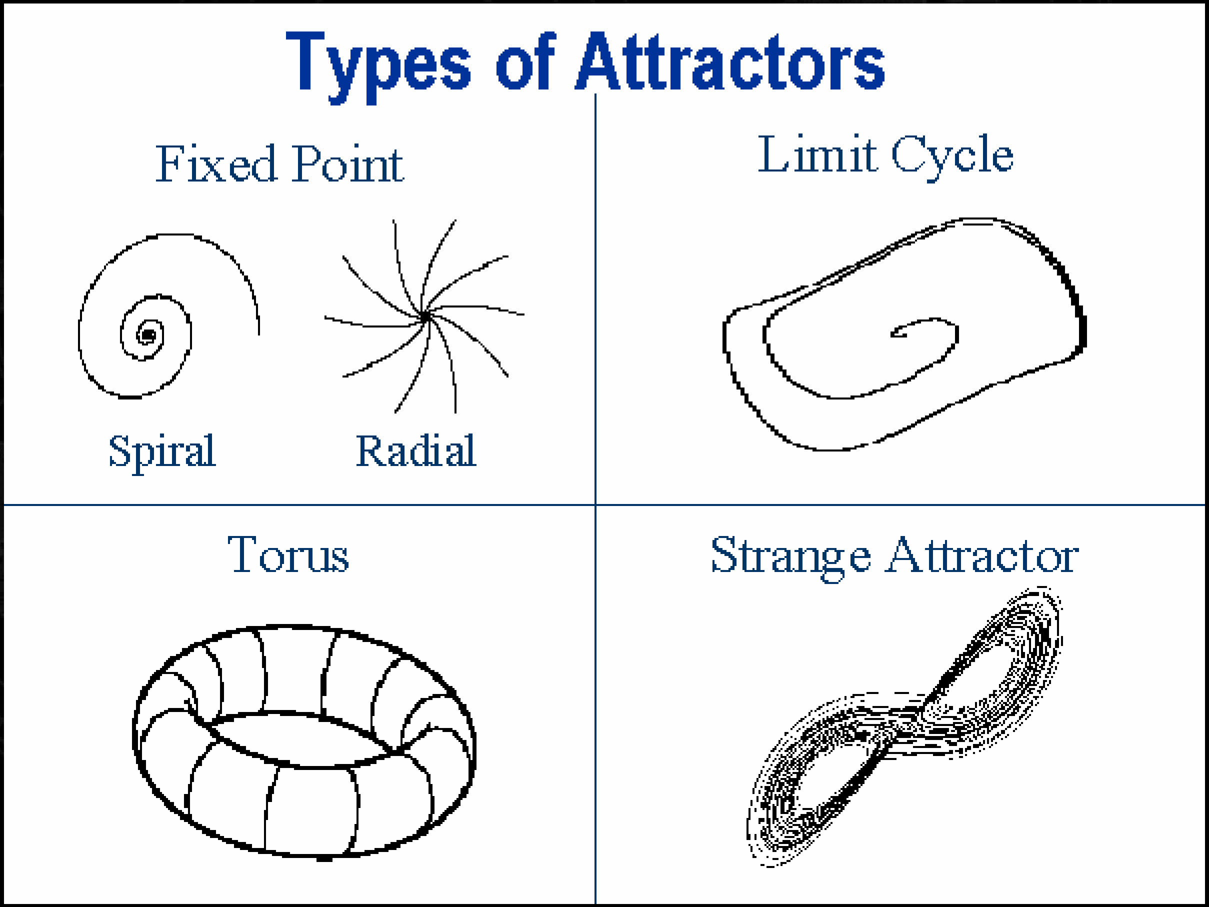
Types of Attractors

Fixed point

Limit cycle

Quasi-periodic

Strange



Types of Attractors

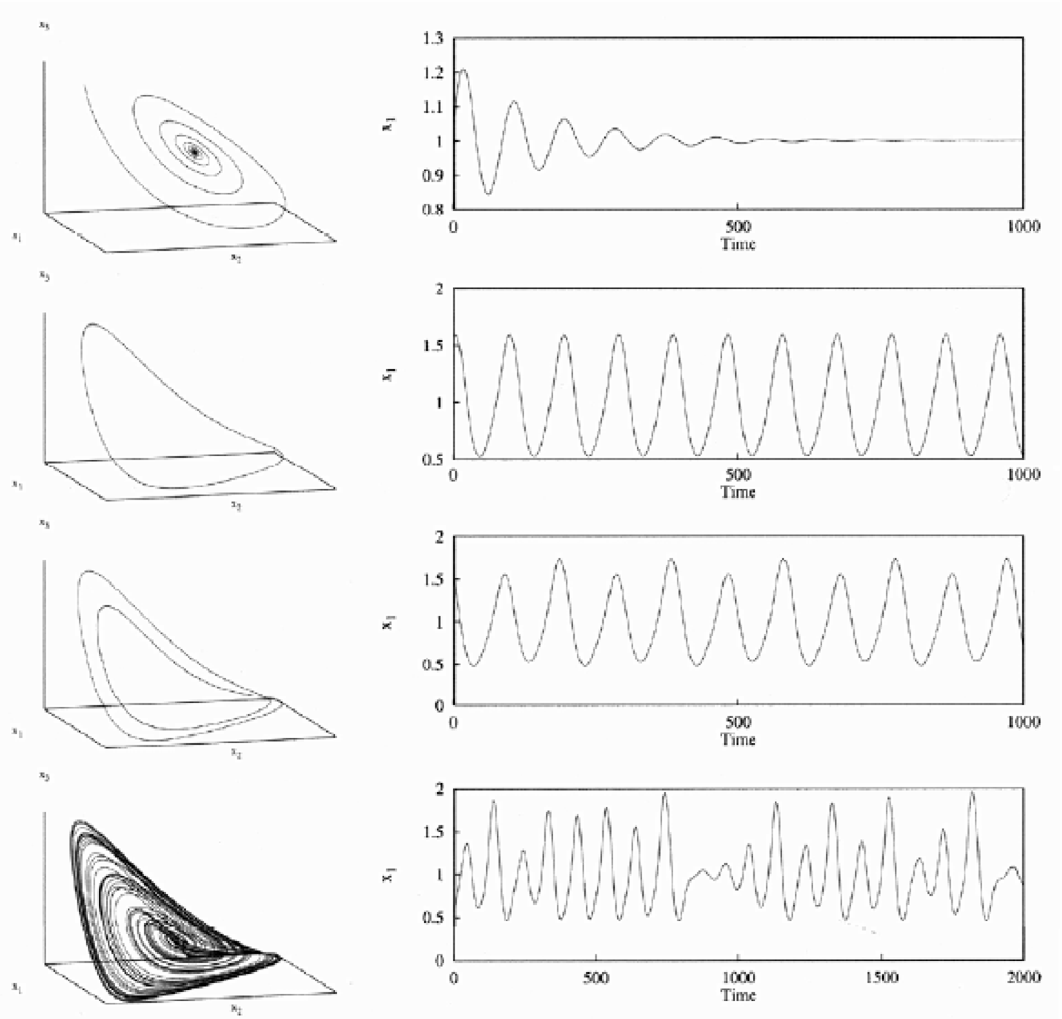
(a) Fixed points

(b) Simple periodic orbits

(c) Period-n orbit

Quasi-periodic

(d) Chaos



Fix-Point Behavior

- 0-dimensional attractor
- Volume of phase space to which the system converges after a long enough time = basin of attraction (defined by all trajectories leading into the attractor)
- Example: Pendulum when friction and gravity bring its motion to a halt

Limit Cycle Behavior

- Periodic motion
- Repetitive oscillation among a number of states (e.g. loop)
- Example: lone planet orbiting around a star in an elliptical orbit

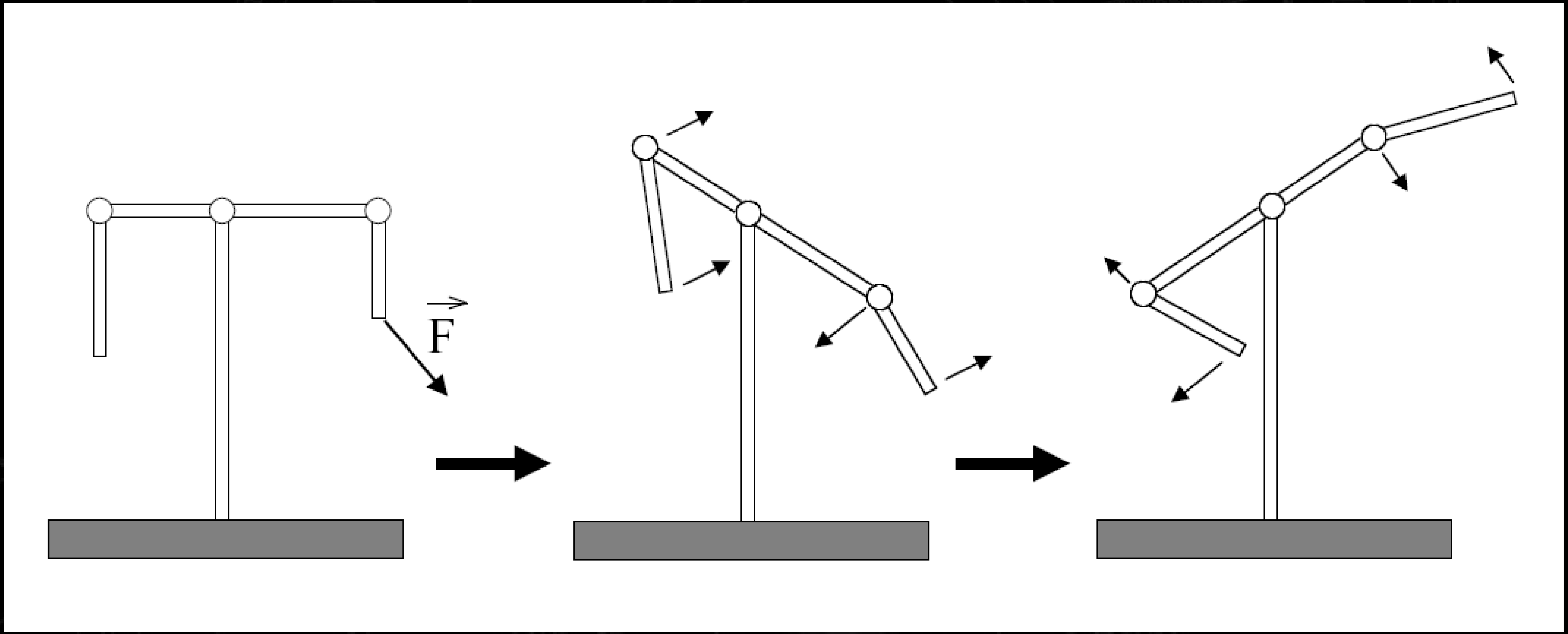
Quasi-Periodic Attractor

- Several independent cyclic motions
- Never quite repeat themselves
- Toroidal attractors
- Example: the moon orbits Earth, which orbits the sun, which, in turn, orbits the galactic center

Strange or Chaotic Attractors

- Pervasive (chaos is everywhere: weather patterns, human brain's electrochemical activity, …)
- Sensitivity to initial conditions (Butterfly effect)
- Deterministic chaos (if we could know the exact initial conditions, trajectories would be determined)
- Low-dimensional chaos (strange attractors are restricted to small volumes of phase-space)
- Weak causality
  - 3-body problem (any slight measurement difference results in very different predictions)
  - Butterfly effect (Lorenz attractor)

Simple Chaotic Systems in Physics



Strange Attractors

Limit set as $t \to \infty$

Set of measure zero

Basin of attraction

Fractal structure

- non-integer dimension
- self-similarity
- infinite detail

Chaotic dynamics

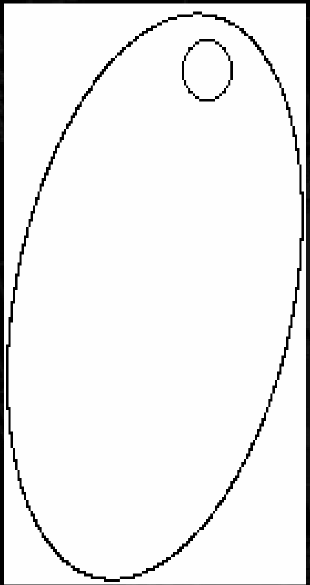
- sensitivity to initial conditions
- topological transitivity
- dense periodic orbits

Aesthetic appeal

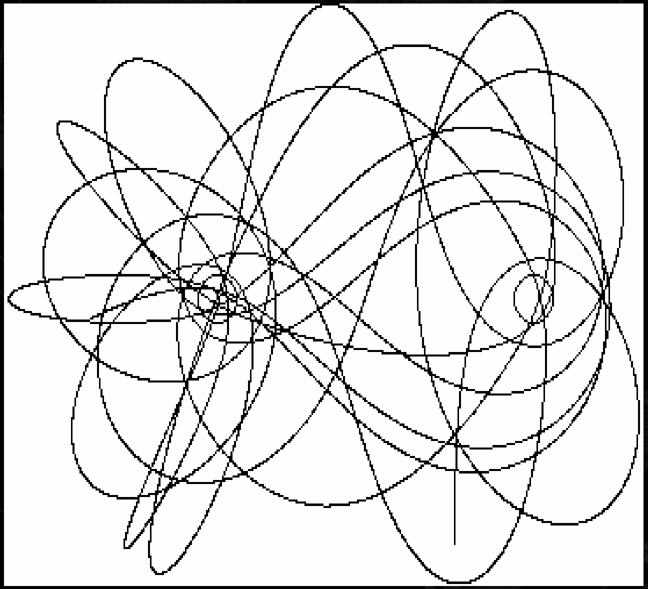
Characteristics of Chaos

- Never repeats
- Depends sensitively on initial conditions (Butterfly effect)
- Allows short-term prediction but not long-term prediction
- Comes and goes with a small change in some control knob
- Usually produces a fractal pattern
- Not random (or stochastic); unpredictable in the short-term but "predictable" in the long-term ...

Example 1: A Planet Orbiting a Star



Elliptical Orbit



Chaotic Orbit

Example 2: The Logistic Map

Also known as the quadratic map or the Feigenbaum map

Simple population growth model defined by the iterative map: $x(t+1) = rx(t)*(1-x(t))$, $0 < r < 4$, $0 < x < 1$ (r = reproduction rate or bifurcation parameter)

if $x = 0$: population is extinct

if $x = 1$: population will be extinct at the next time step

$rx(t)$ → positive feedback term

$1-x(t)$ → negative feedback term (decrease to overpopulation)

Example 2: The Logistic Map

Question: What happens to the long-term behavior of x(t) for different values of ‘r’?

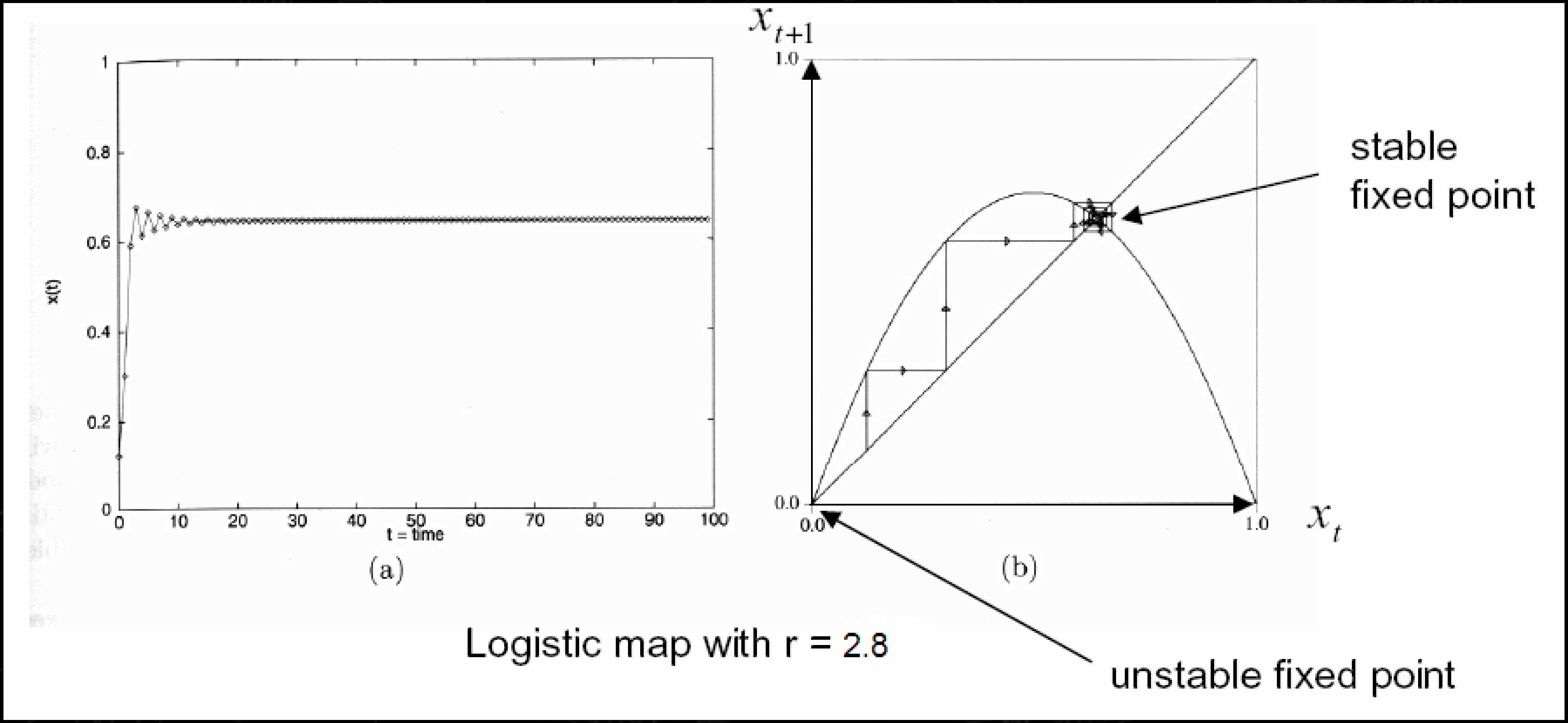
Special cases:

0<r<1: all terms <1 → extinction

1<r<3: fix point behavior

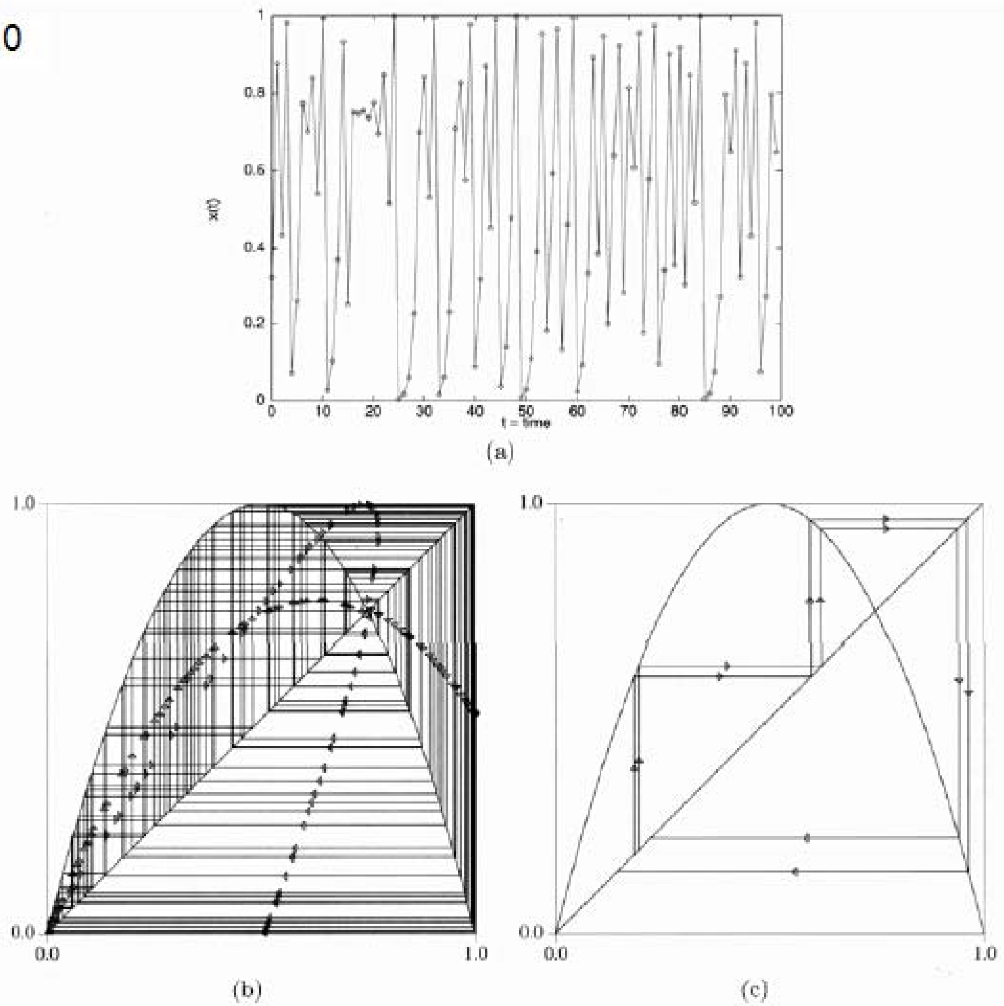
r>3: period doubling (bifurcation)

Logistic Map – Fix Point



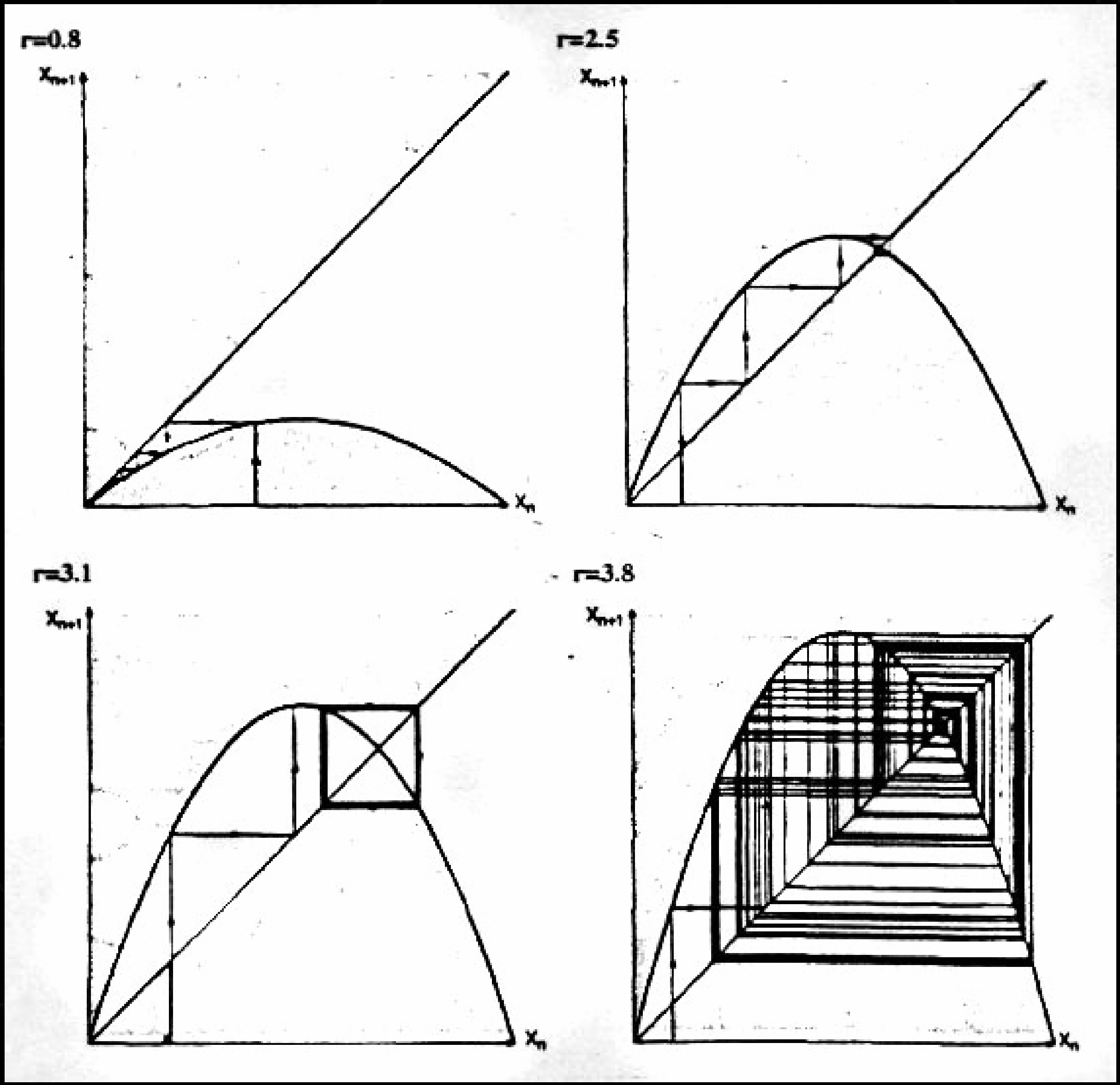
Logistic Map – Chaos

Logistic map with r = 4.0

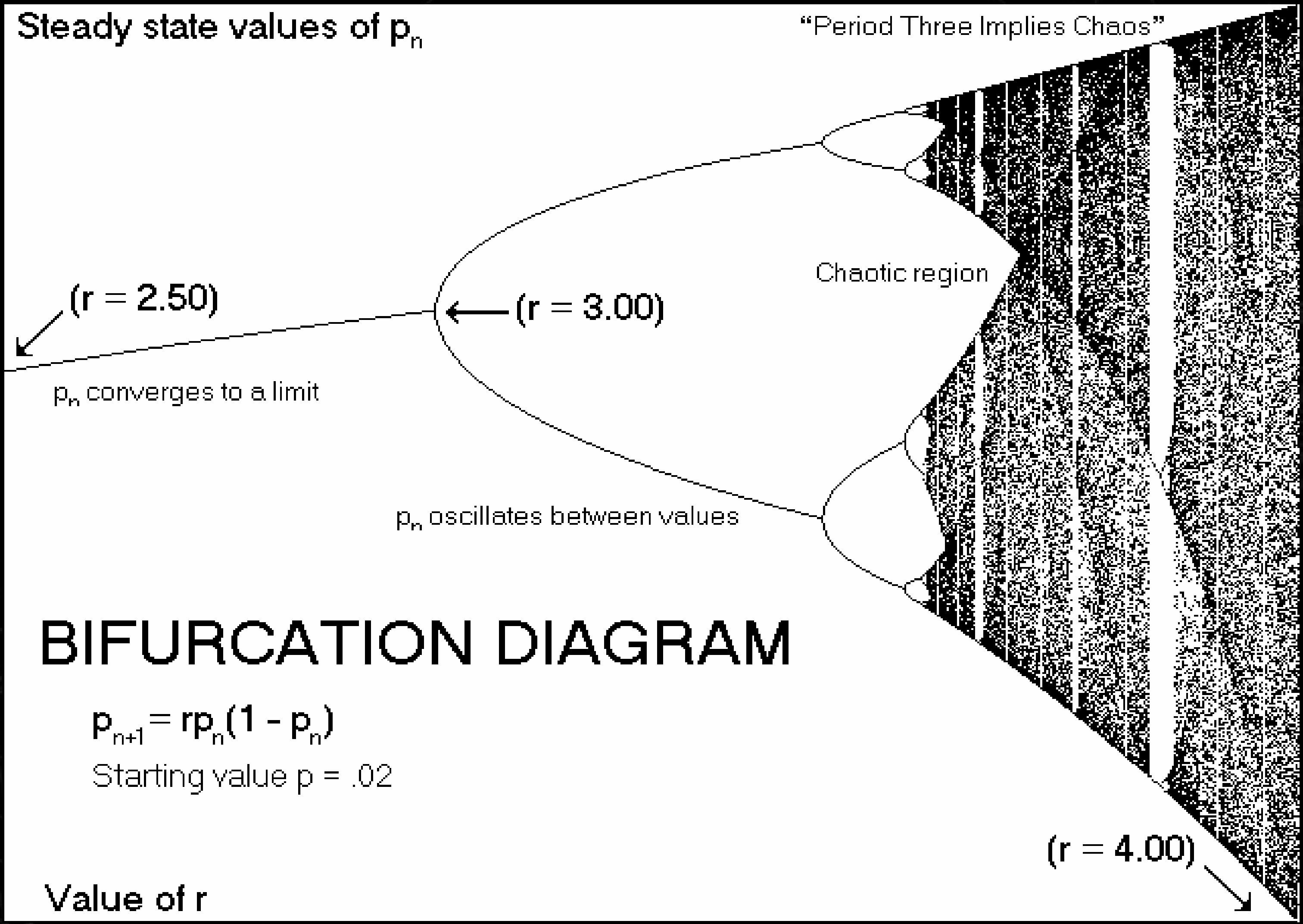


Cobweb plot at: http://www.emporia.edu/math-cs/yanikjoe/Chaos/CobwebPlot.htm

The Logistic Map – Four Types of Attractors

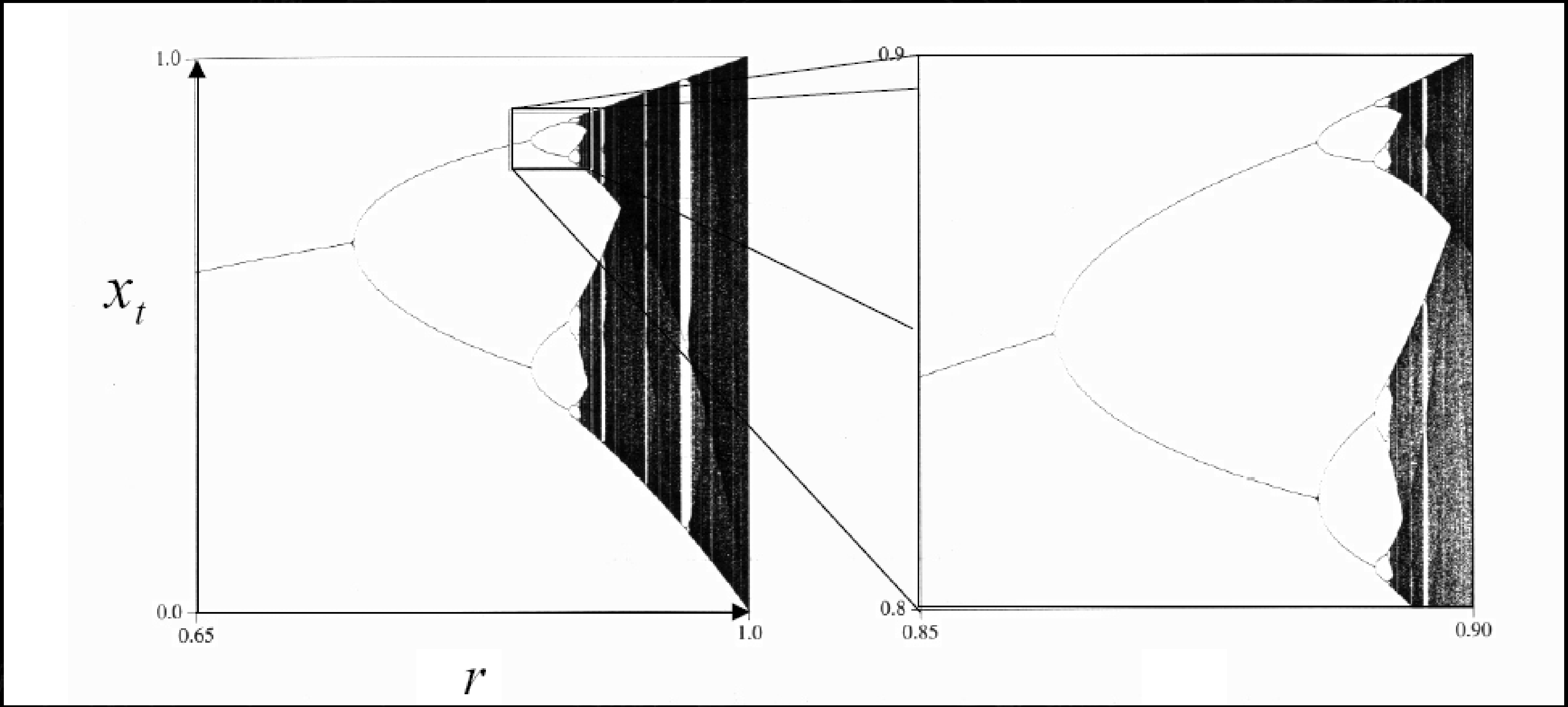


The Logistic Map – Bifurcation Diagram



DEMO: http://www.emporia.edu/math-cs/yanikjoe/Chaos/Bifurcation.htm

Logistic Map – Bifurcations and Self-Similarity



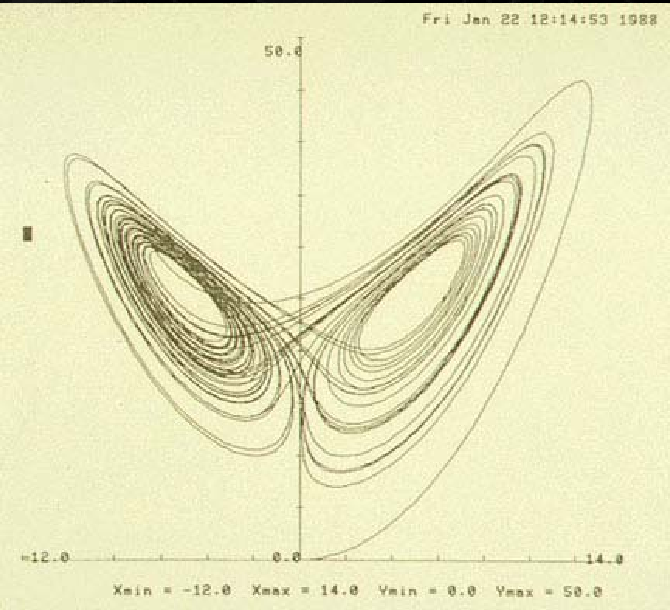
Example 3: Lorenz Attractor

Discovered sensitivity to initial conditions in a simple 3-variable dynamical system; simplified model of weather; convection flows in the atmosphere (x: convection; y: temperature difference; z: distortion of the temperature profile)

$$\frac{dx}{dt} = \sigma(y-x)$$

$$\frac{dy}{dt} = rx-y-xz$$

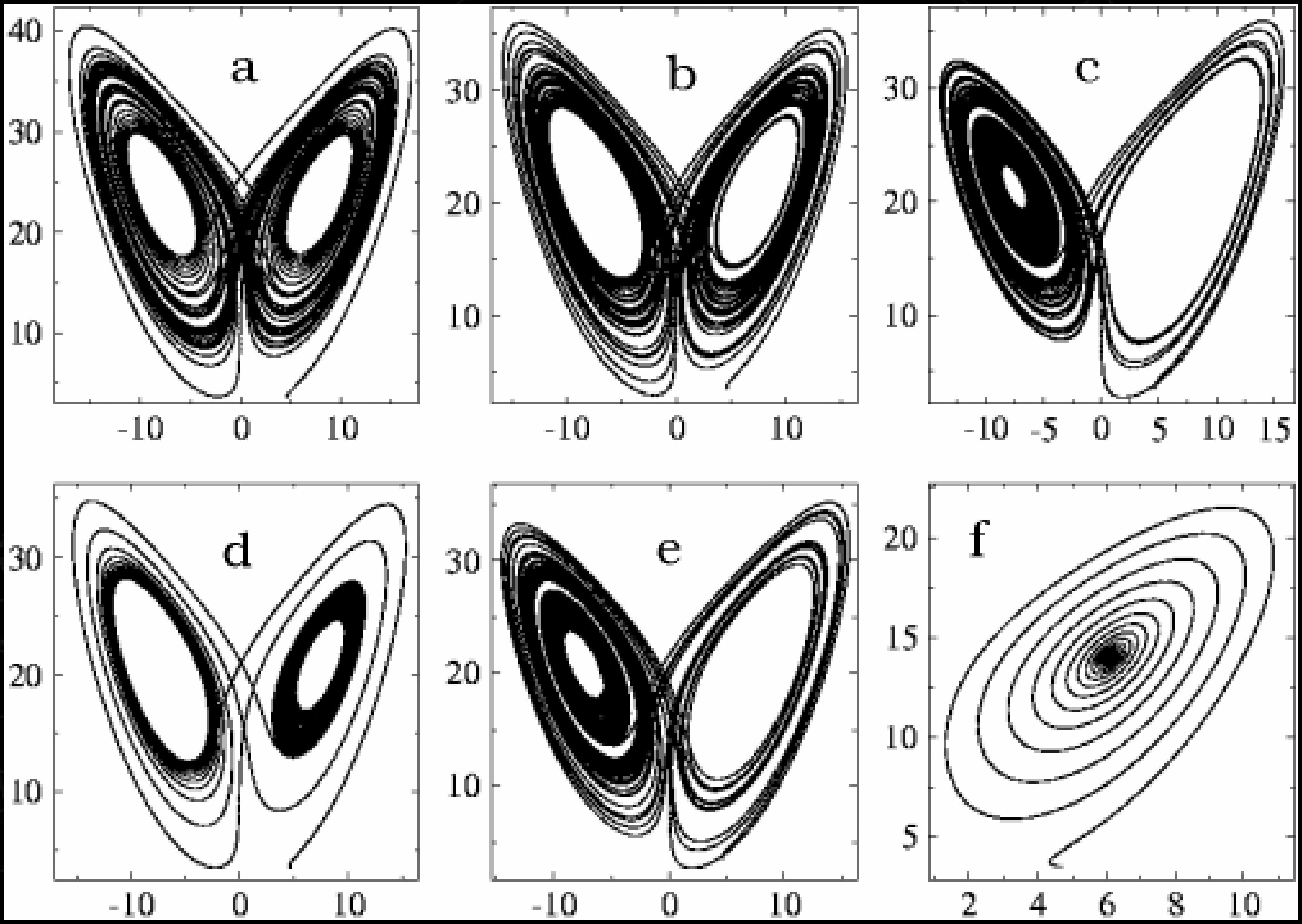
$$\frac{dz}{dt} = xy-bz$$



DEMO: http://www.cmp.caltech.edu/~mcc/Chaos_Course/Lesson1/Demo8.html

DEMO: http://www.cmp.caltech.edu/~mcc/chaos_new/Lorenz.html

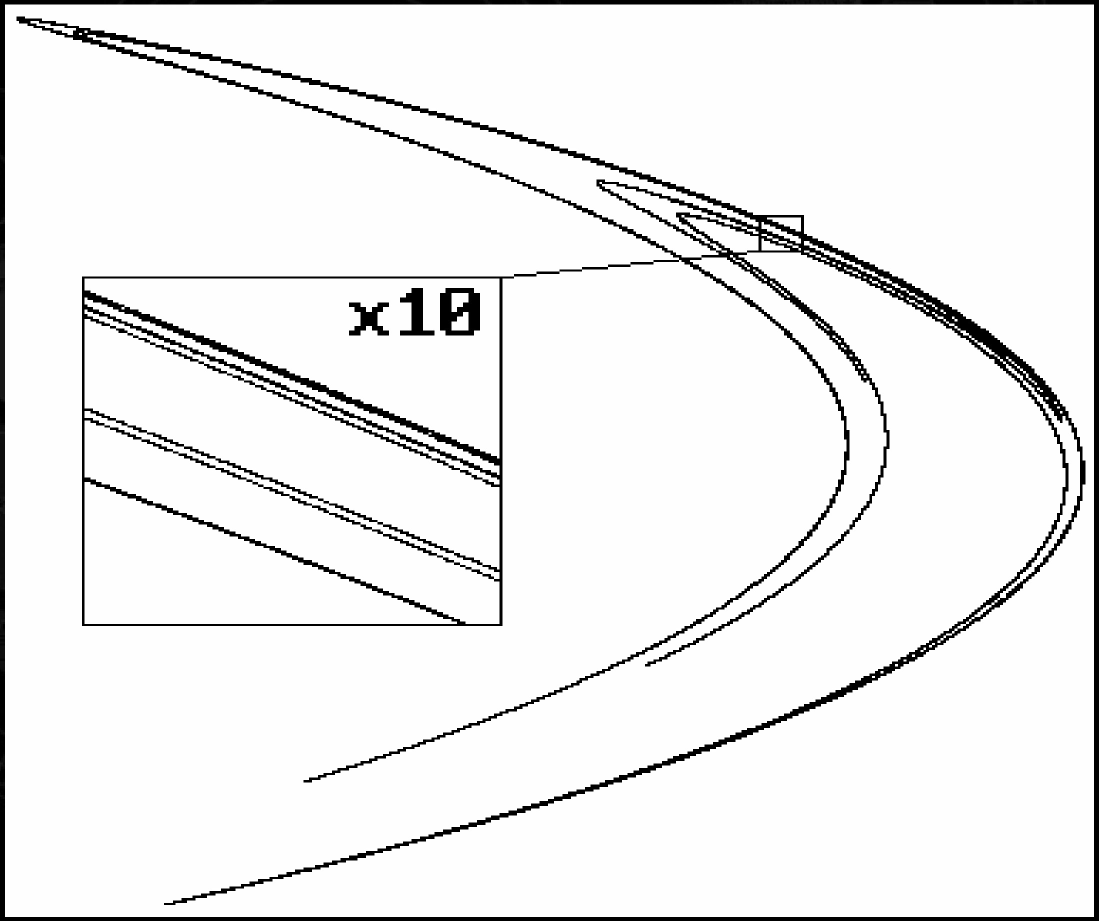
Example 3: Lorenz Attractor



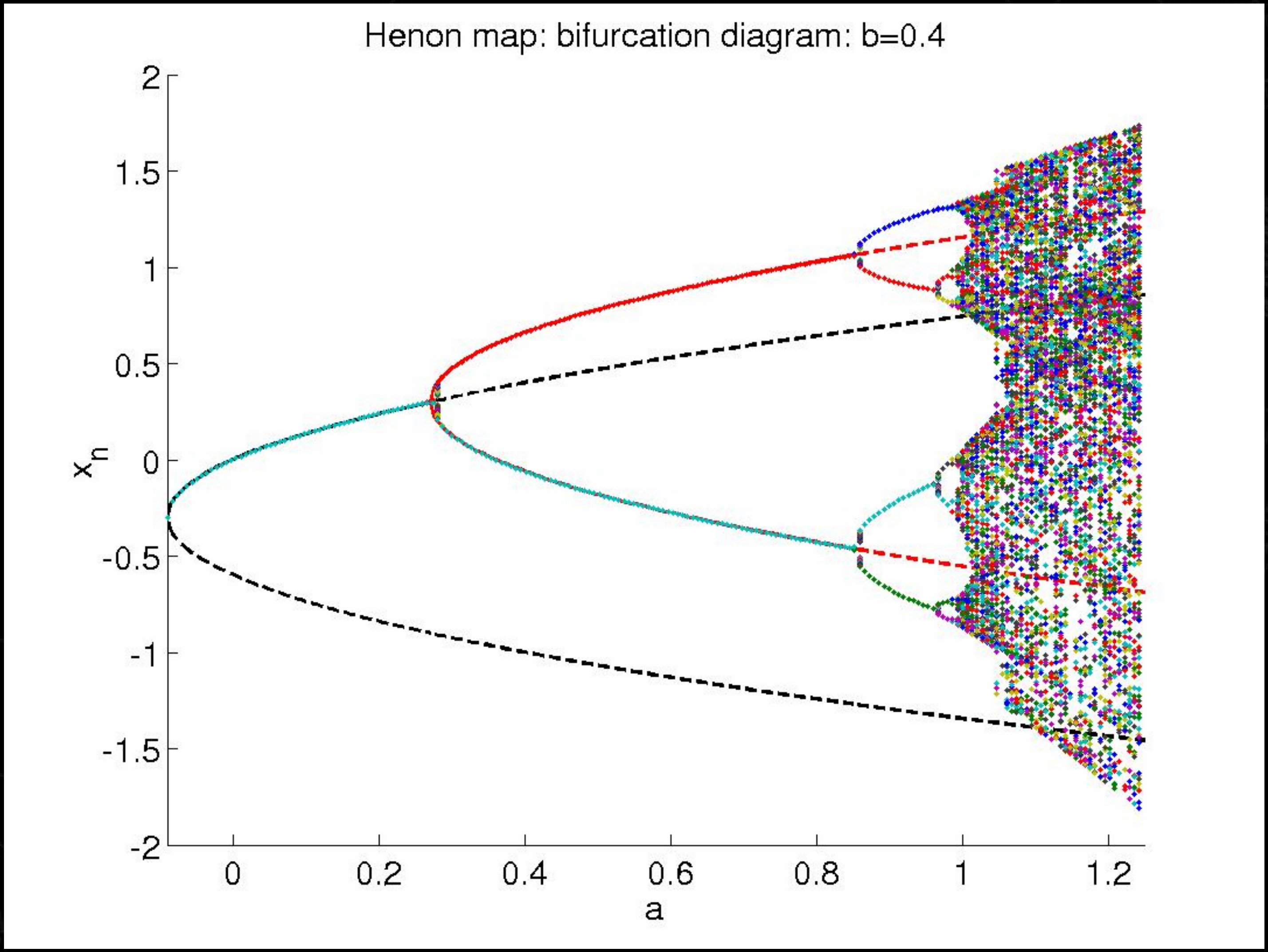
Example 3: The Hénon Attractor

$$x_{n+1} = a - x_n^{\,2} + b x_{n-1}$$

Example of infinite detail …



Example 3: The Hénon Attractor



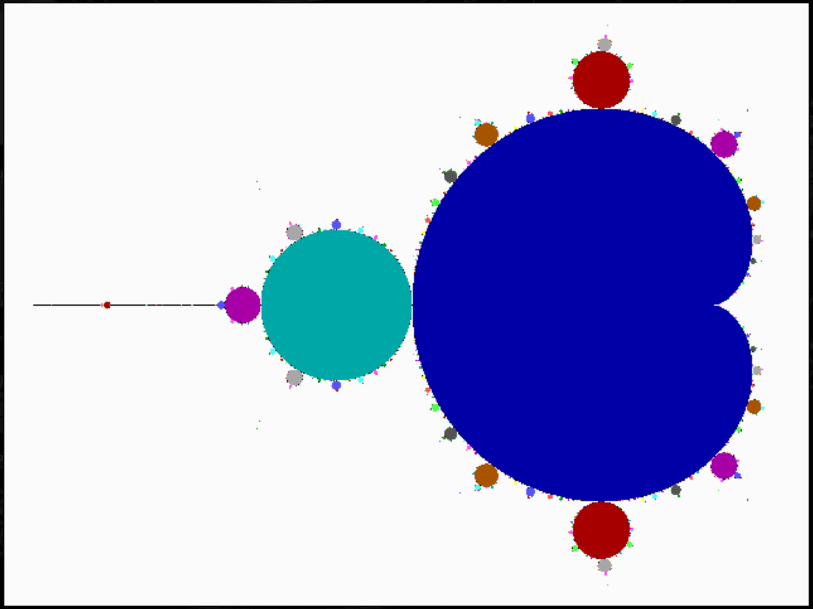
Example 4: General 2-D Quadratic Map

$$x_{n+1} = a_1 + a_2 x_n + a_3 x_n^2 + a_4 x_n y_n + a_5 y_n + a_6 y_n^2$$

$$y_{n+1} = a_7 + a_8 x_n + a_9 x_n^2 + a_{10} x_n y_n + a_{11} y_n + a_{12} y_n^2$$

$$x_{n+1} = x_n^2 - y_n^2 + a$$

$$y_{n+1} = 2 x_n y_n + b$$



a

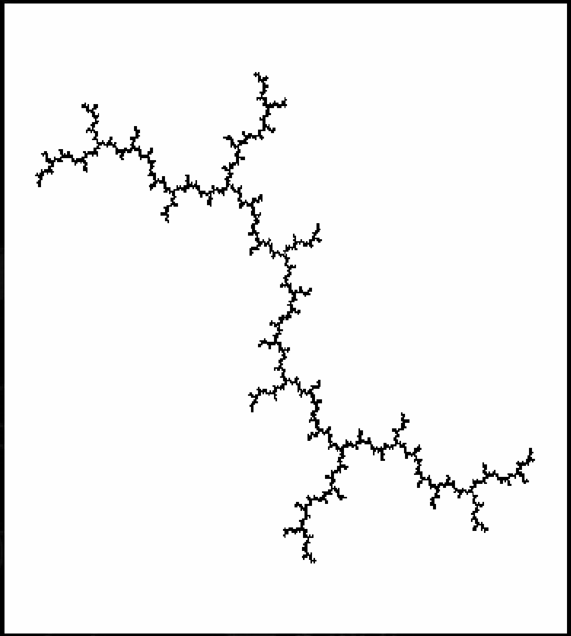
b

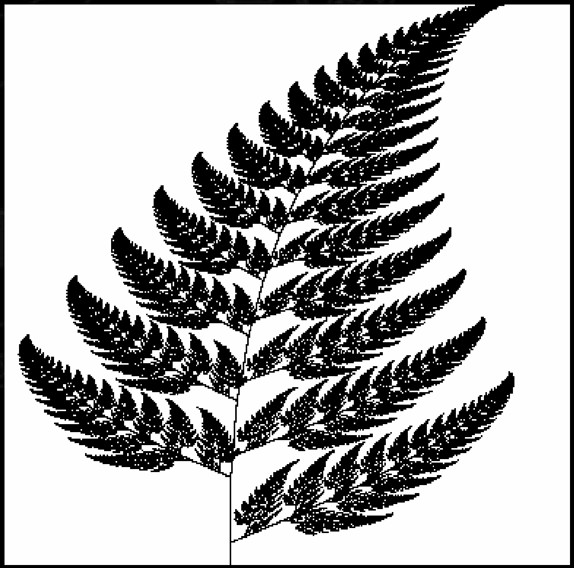
Take-Home-Message

- Simple equations can give rise to complex behavior
- Chaotic systems are deterministic and not random (but also unpredictable in the long-term; prediction in the short-term fairly accurate)
- Chaotic systems are extremely sensitive to the initial conditions
- Presence of iterations
- The devil is in the details

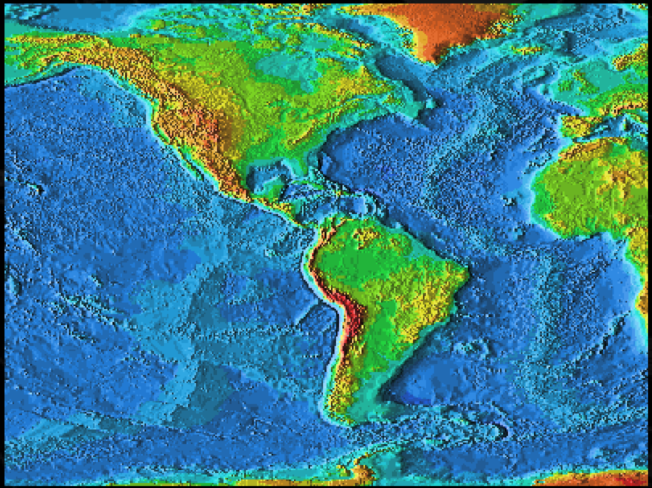
Fractals

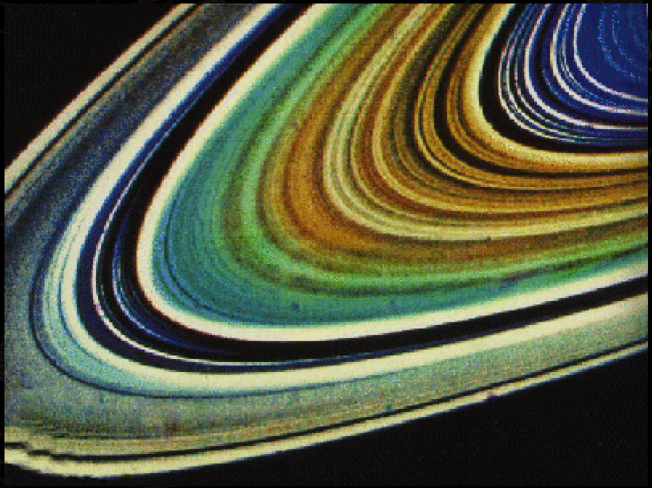
- Termed coined by Benoit Mandelbrot to differentiate pure geometric figures (circle, square, …) from other types of figures that defy such simple classification
- Structure on all scales (detail persists when zoomed arbitrarily)
- Geometrical objects generally with non-integer dimension
- Self-similarity (contains infinite copies of itself)



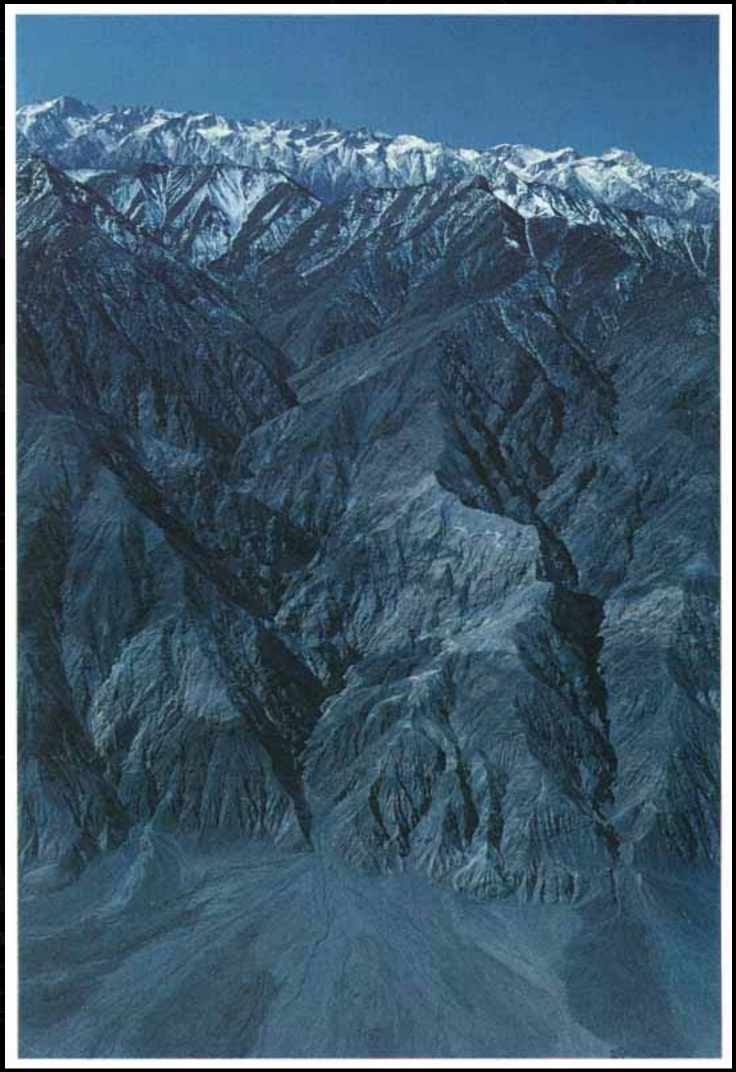


Fractals in Nature





Which One is Digital?

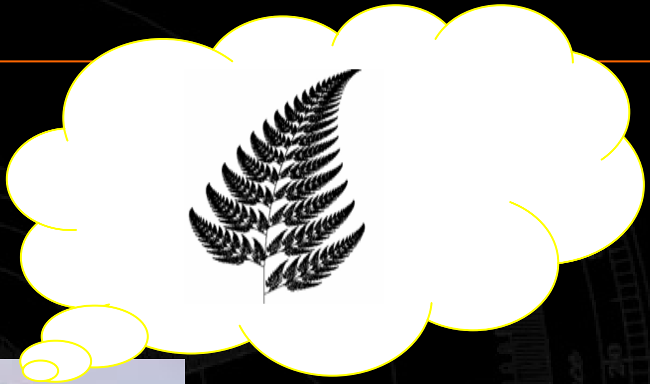


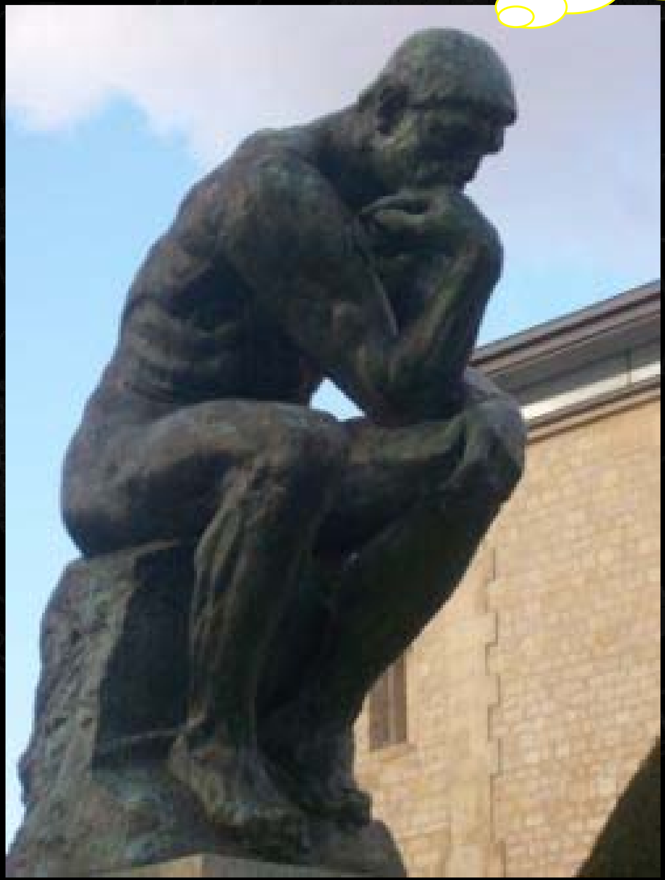
Fractals in the Human Body

(a) (b) (c)

Figure 2.5 Naturally occurring fractals in the human body: (a) brain, (b) lungs, (c) kidney

Properties: Anyone?





Properties

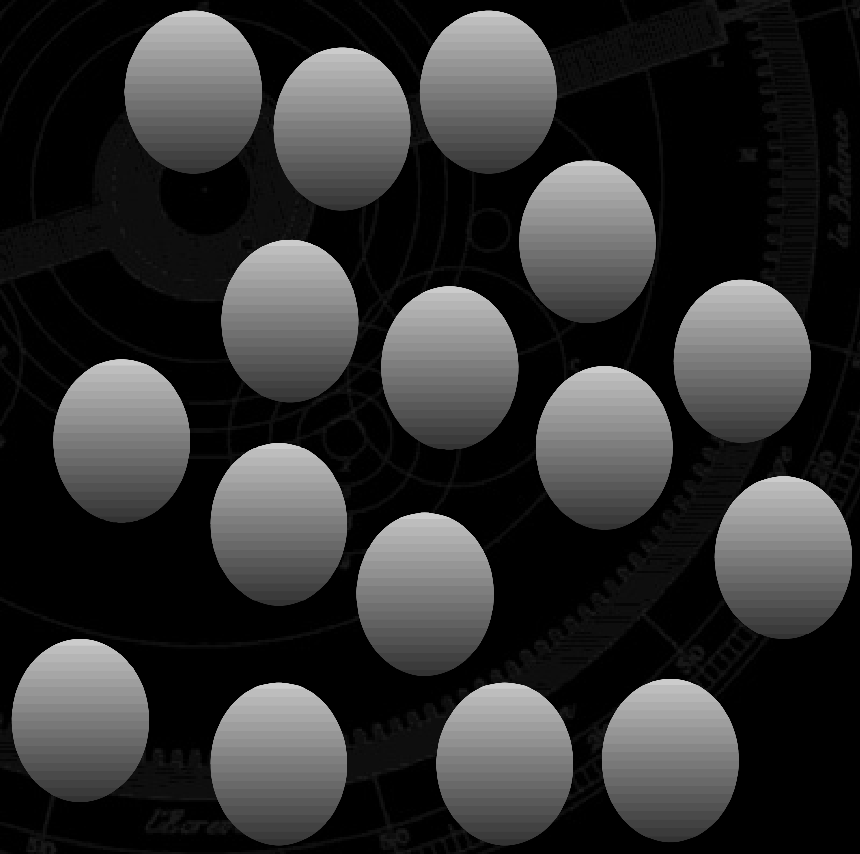
- They are fractal! ☺
- Display self-similarity
- Display scale-invariance

Non-Fractal

Size of features

1 cm

1 characteristic scale



Fractal

Structure on all scales (detail persists when zoomed arbitrarily)

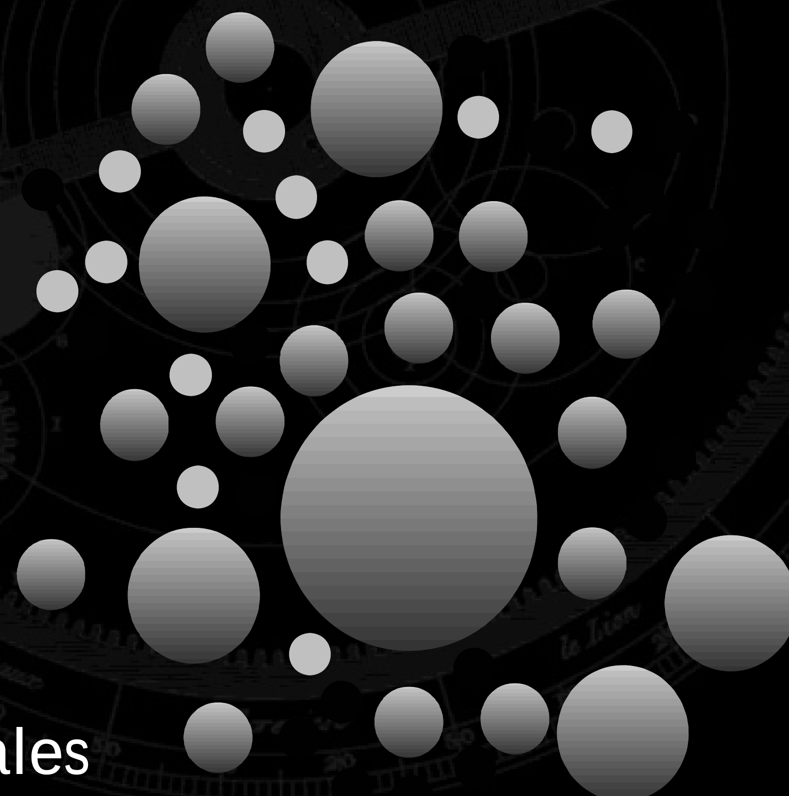
Size of features

2 cm

1 cm

1/2 cm

1/4 cm



many characteristic scales

Self-Similarity and Scale-Invariance

- *"When each piece of a shape is geometrically similar to the whole, both the shape and the cascade that generate it are called self-similar."* (B. Mandelbrot)
- Contains infinite copies of itself
- Scaling/Scale = The value measured for a property does not depend on the resolution at which it is measured
- Two types of invariance:
  - Geometrical
  - Statistical

Important Concept

Self-Similarity and Scale-Invariance

Self-Similarity and Scale Invariance

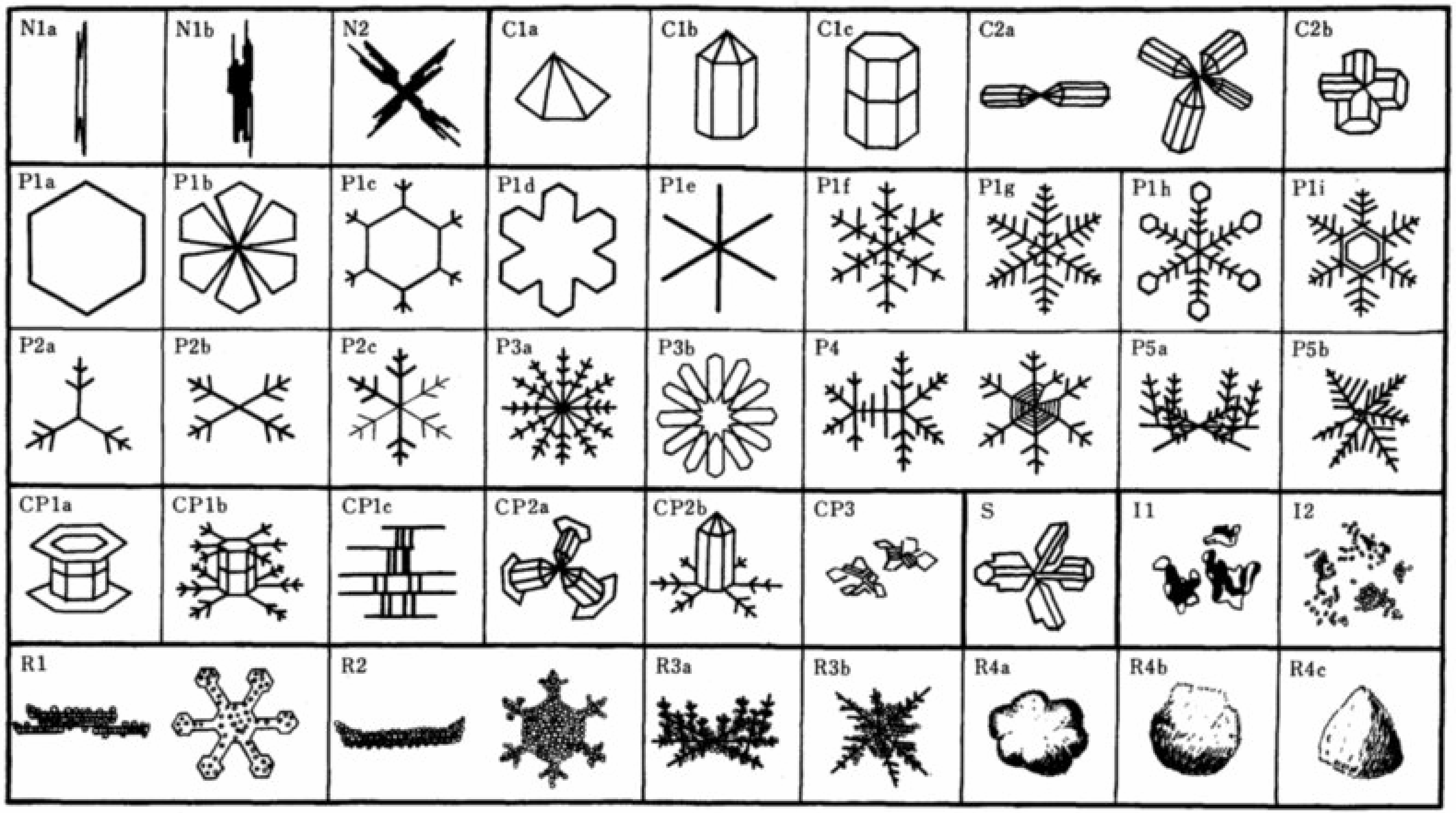


FIG. 197. General classification of snow crystals, sketches.

Scale-Invariance

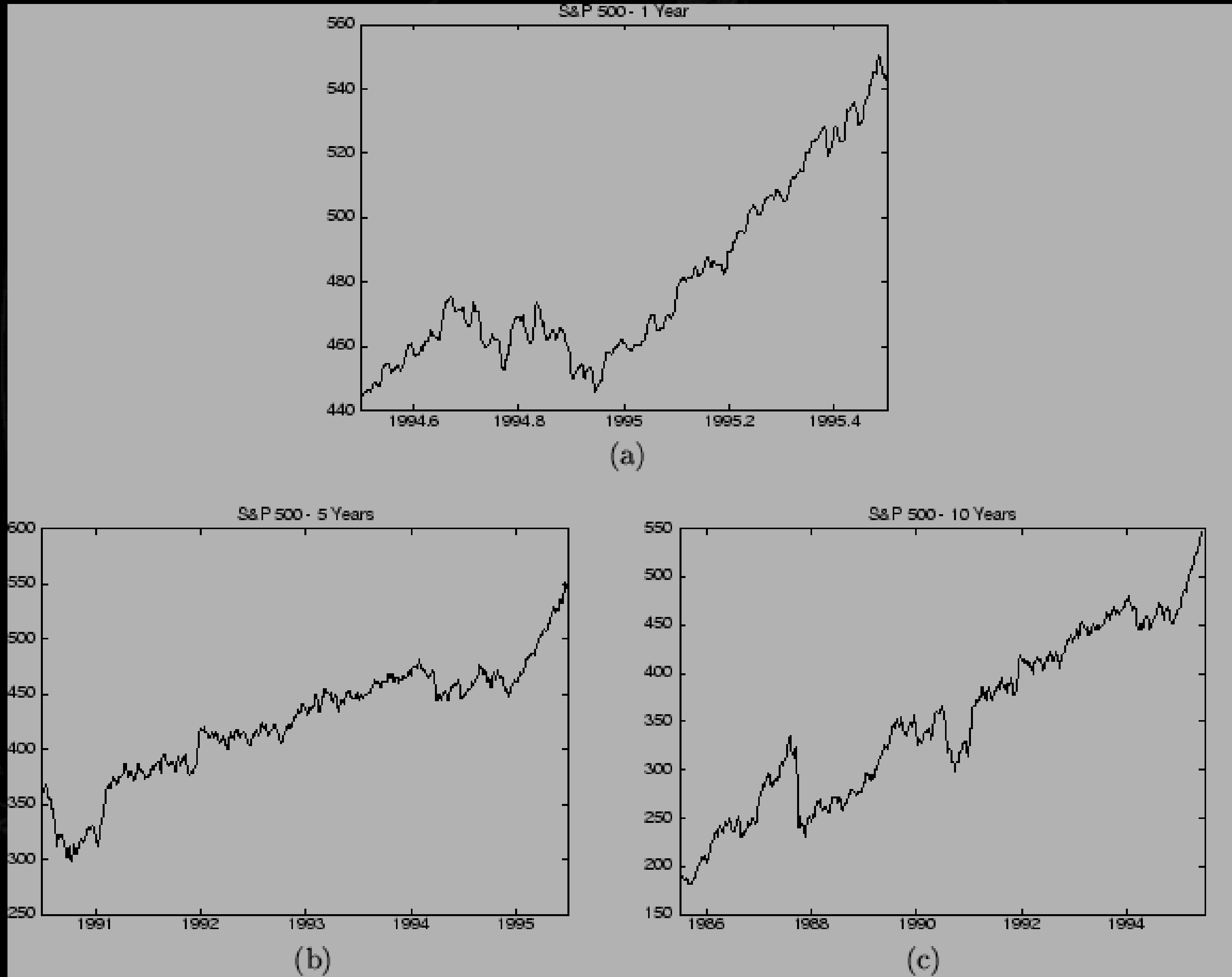
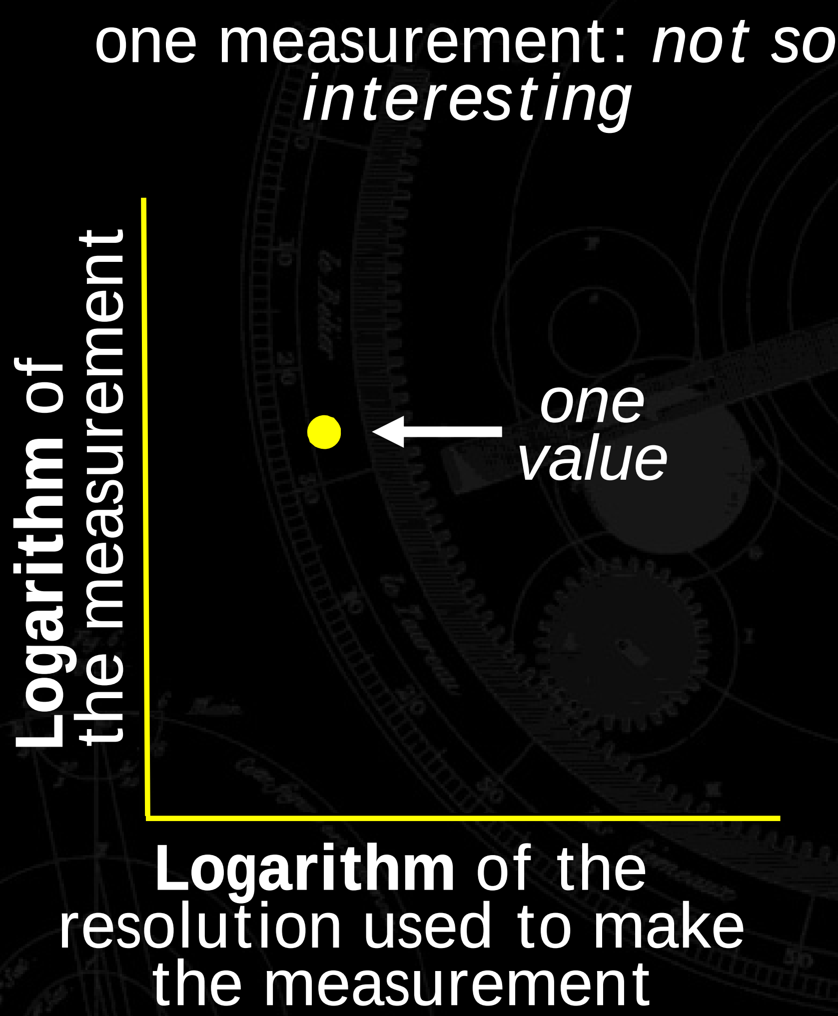
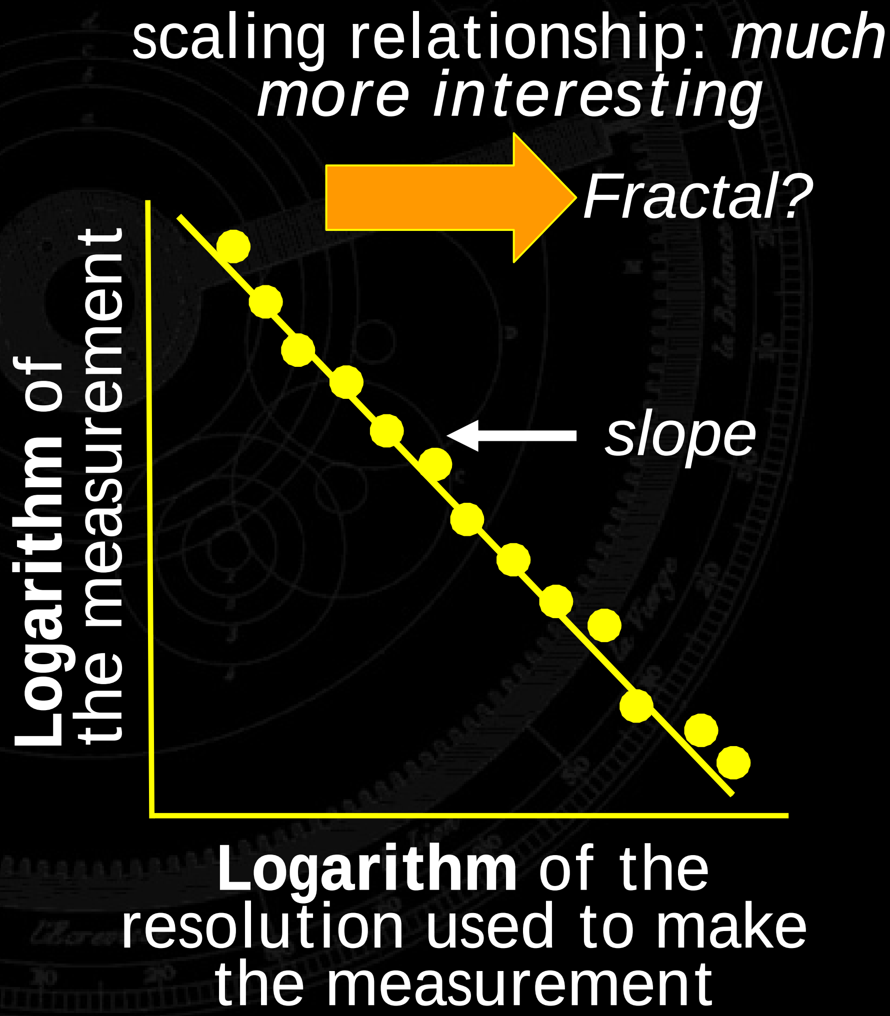


Figure 2.7 The S&P 500 stock index shown on various time scales. (a) one year, (b) five years, (c) ten years

Scaling


one measurement: *not so interesting*
Logarithm of the measurement
one value
Logarithm of the resolution used to make the measurement


scaling relationship: *much more interesting*
Fractal?
Logarithm of the measurement
slope
Logarithm of the resolution used to make the measurement

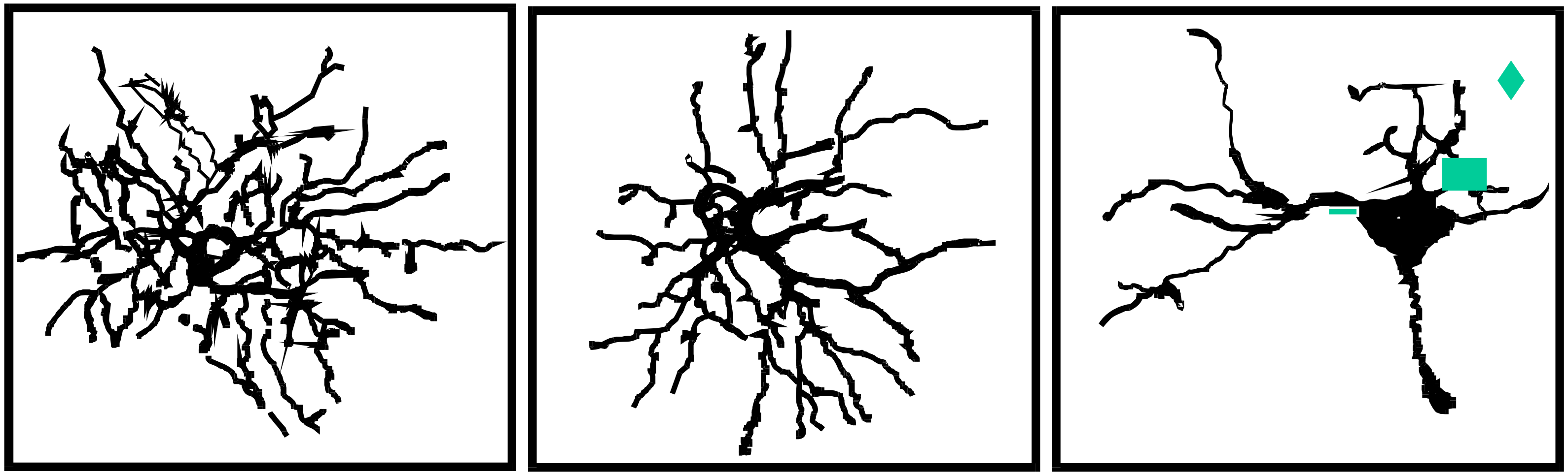
Why Fractals?

- Packing efficiency: fractals are very good at squeezing a great deal length (or surface) – perhaps infinite – into a small finite area
- Reason: minimize material requirements while maximizing functionality

Branching Patterns

nerve cells

in the retina, and in culture



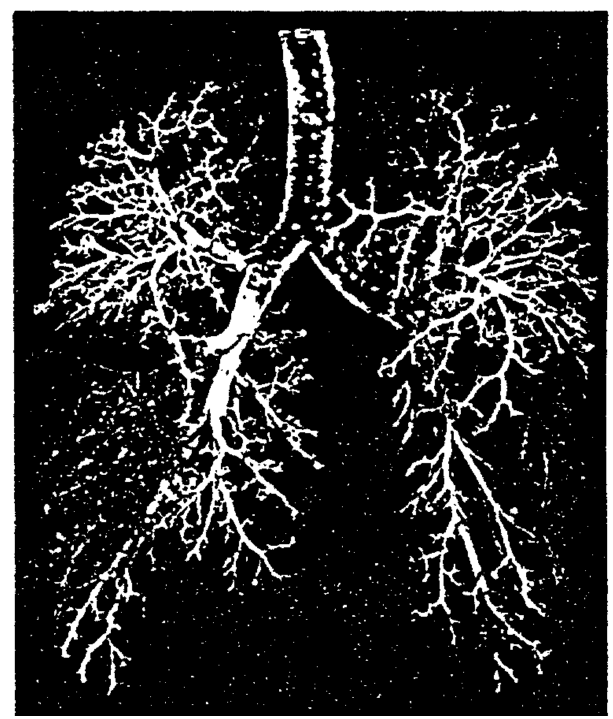
Branching Patterns

blood vessels
in the retina

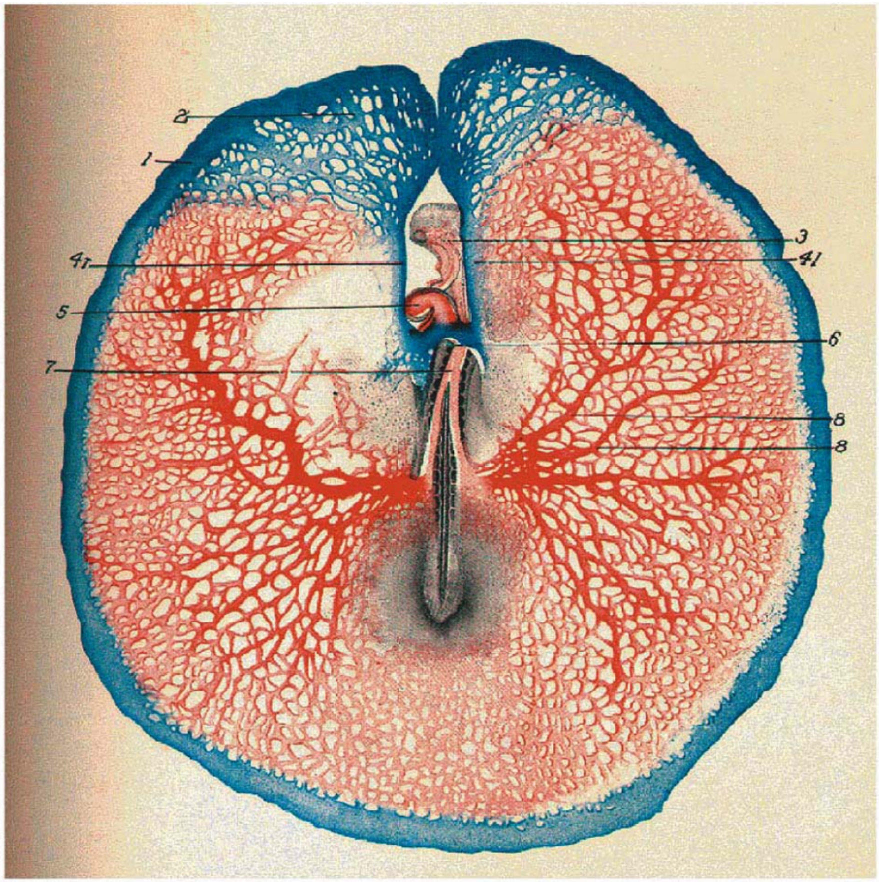
Family, Masters, and Platt 1989
Physica D38:98-103
Mainster 1990 Eye 4:235-241

air ways
in the lungs

West and Goldberger 1987
Am. Sci. 75:354-365



Branching Patterns

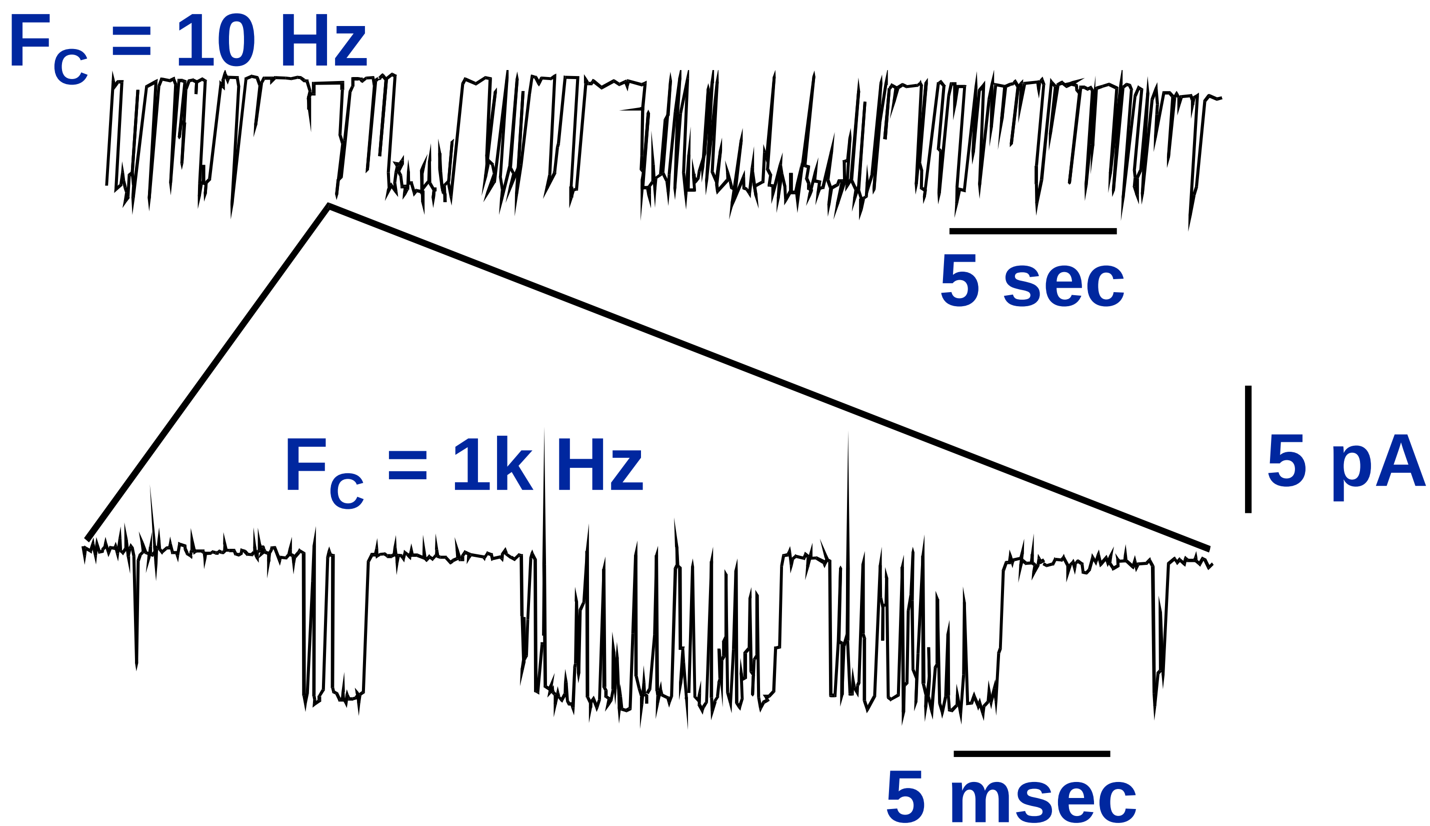


DEVELOPMENTAL BIOLOGY, Eighth Edition, Part 1, C

Currents Through Ion Channels

ATP sensitive potassium channel in β cell from the pancreas

Gilles, Falke, and Misler (Liebovitch 1990 Ann. N.Y. Acad. Sci. 591:375-391)



How Are Fractal Patterns Generated?

How are fractals grown?

Three known mechanisms

- Iteration
- Diffusion
- Recursion

Example: The Cantor Set (Mathematical Monster)

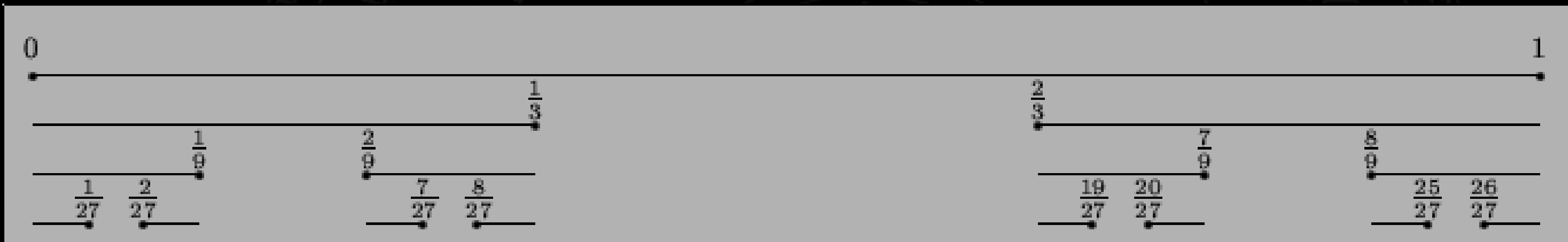


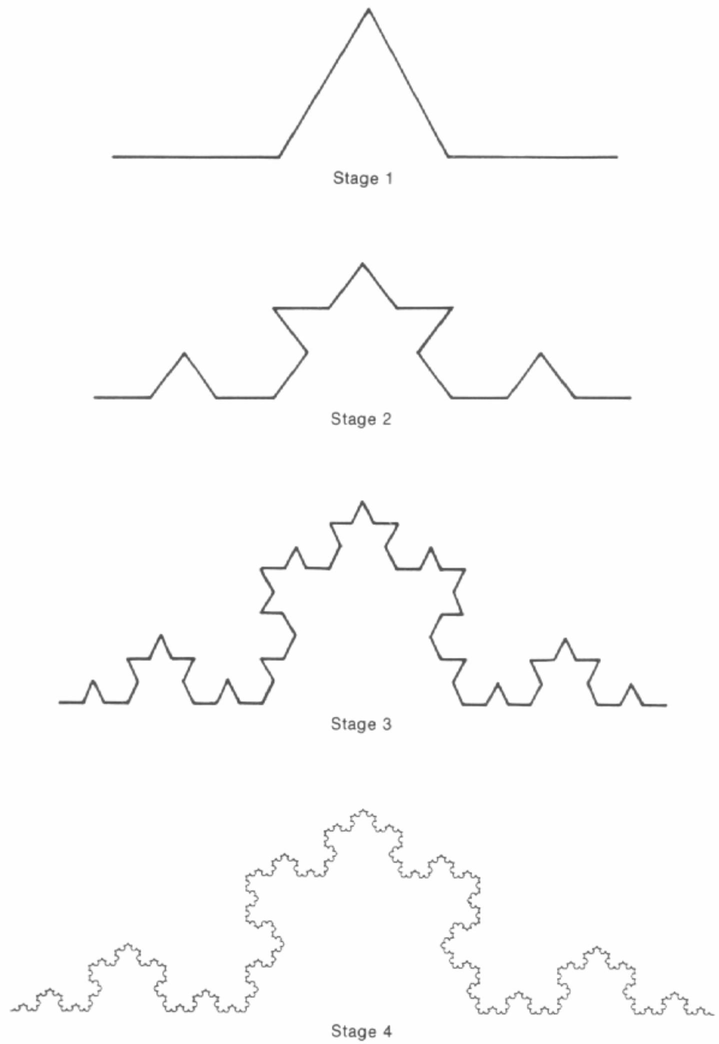
Figure 2.3. The Cantor set with points labeled

Requires: iteration and recursion

Note: points in Cantor set are uncountably infinite but width of all the points is (2/3)^n → 0, for n → 0

Example: The Koch Curve (Math. Monster)

Question: what is the length of the Koch curve after n=100 iterations if the length of one segment is 1m?



Adapted from Benoit Mandelbrot, *Fractals*.

Example: Sierpinski Triangle

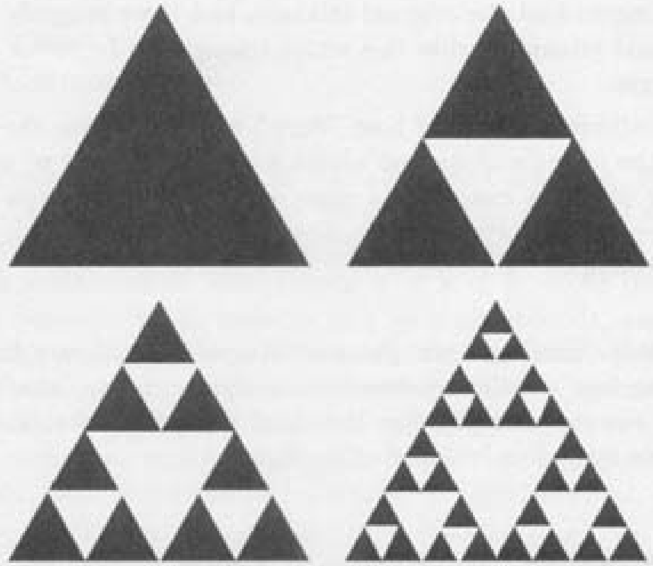


Figure 9.1 Construction of the Sierpinski Triangle.

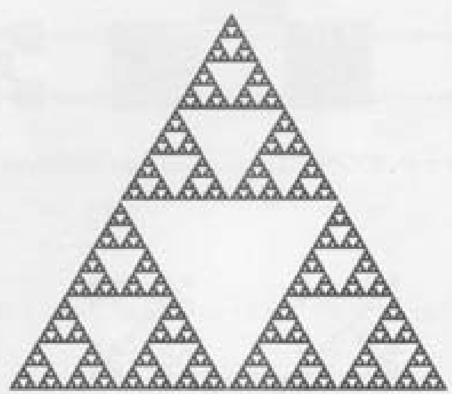
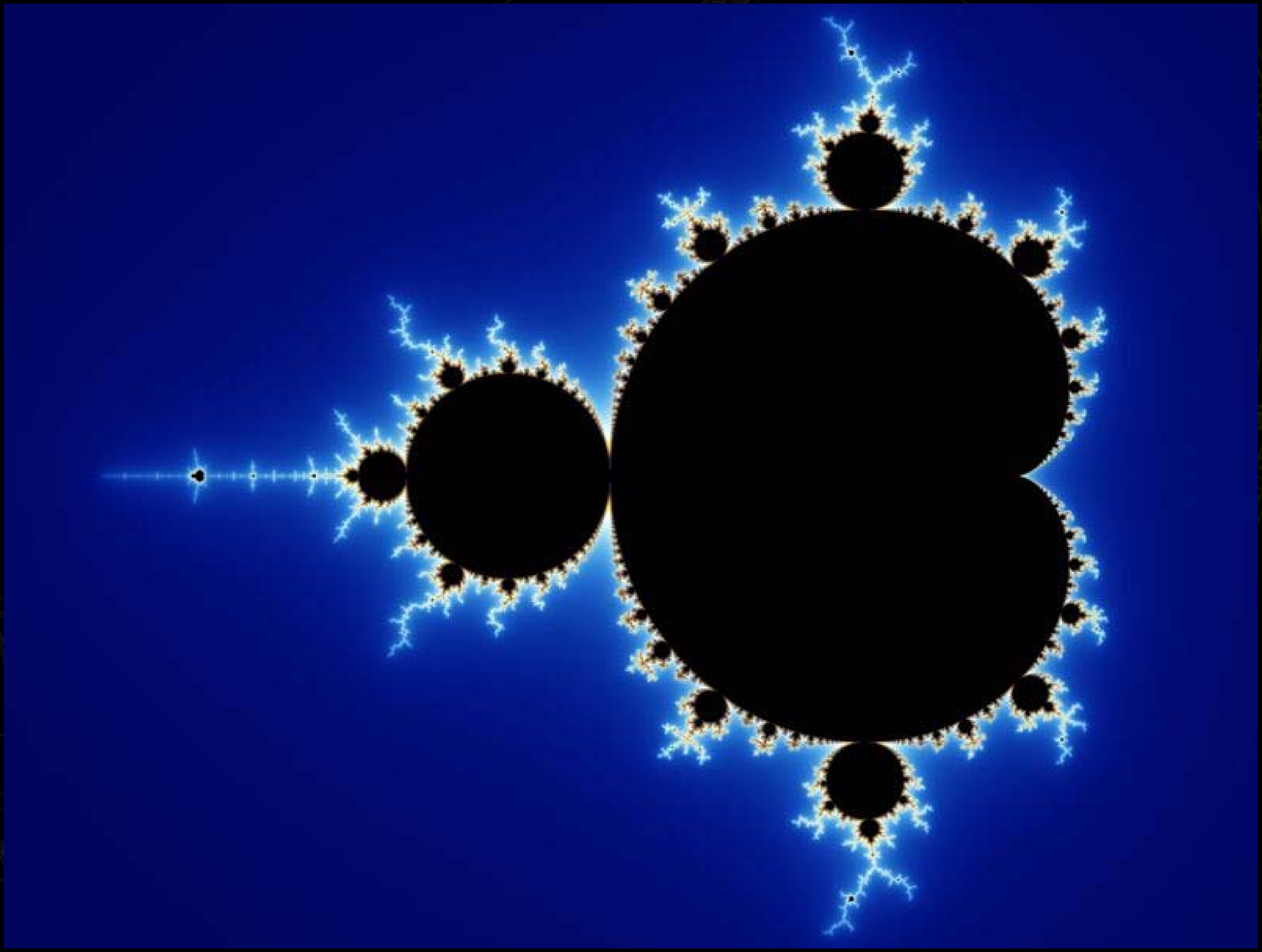


Figure 9.2 The Sierpinski triangle.

Example: The Mandelbrot Set



Example: The Mandelbrot Set

Technically speaking: “iterative dynamical system”

<u>Pseudo-code:</u>

```
For each number, c, in a subset of the complex plane
   Set xt=0
   For t=1 to tmax
        Compute xt = xt^2 + c
        If |xt|>2, then break out of loop
   EndFor
   If t<tmax, then color point c white
   If t=tmax, then color point c black
EndFor
```

Definition: The Mandelbrot set is defined as the set of points that <u>never diverges</u>!

Example: The Mandelbrot Set

Special cases:

1. *c = 0* (origin of complex plane): xt = xt^2 = 0 (stays bounded)
2. *c = i*: x[0] = 0; x[1] = i; x[2] = -1 + i; ...
3. *c = 1+i*: x[t] unbouded (sequence diverges before tmax iterations)
4. *c = 0.01+i* (compare with 2): sequence diverges before tmax iterations

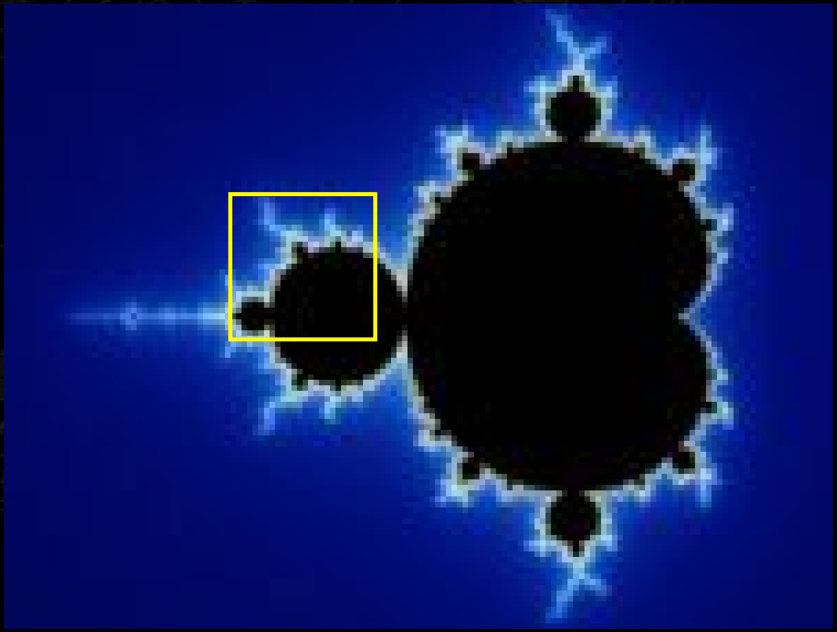
→ Butterfly effect!

Example: The Mandelbrot Set

```
For each pixel on the screen do:
{
   x = a = x co-ordinate of pixel
   y = b = y co-ordinate of pixel
   x2 = x*x
   y2 = y*y
   iteration = 0
   maxiter = 1000
while ( x2 + y2 < (2*2) AND iteration < maxiter )
{
   x = x2 - y2 + a
   y = 2*x*y + b
   x2 = x*x
   y2 = y*y
   iteration = iteration + 1
}
if ( iteration == maxiter )
   color = black
else
   color = iteration
}
```

$$x_{n+1} = x_n^2 - y_n^2 + a$$

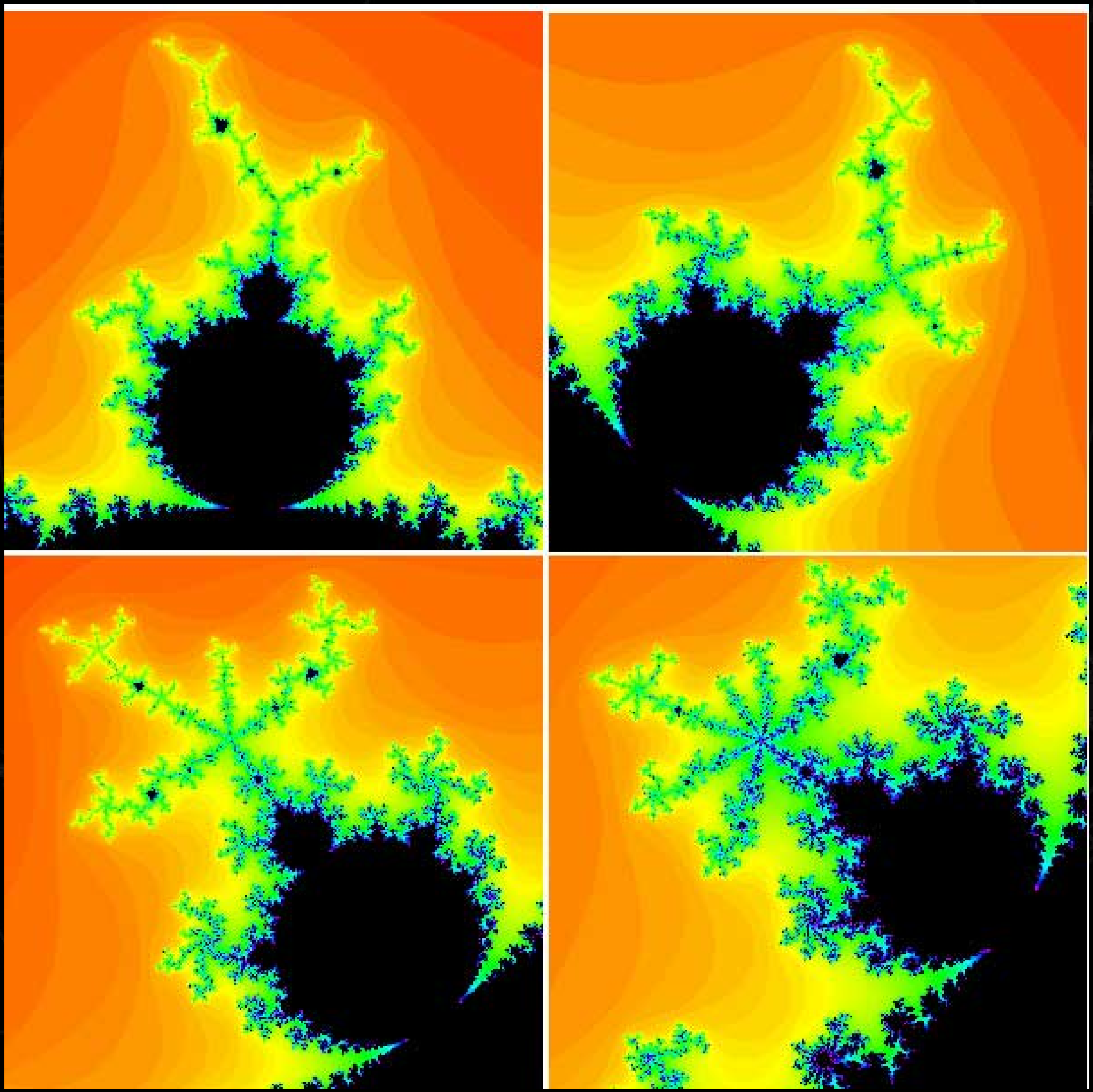
$$y_{n+1} = 2x_n y_n + b$$



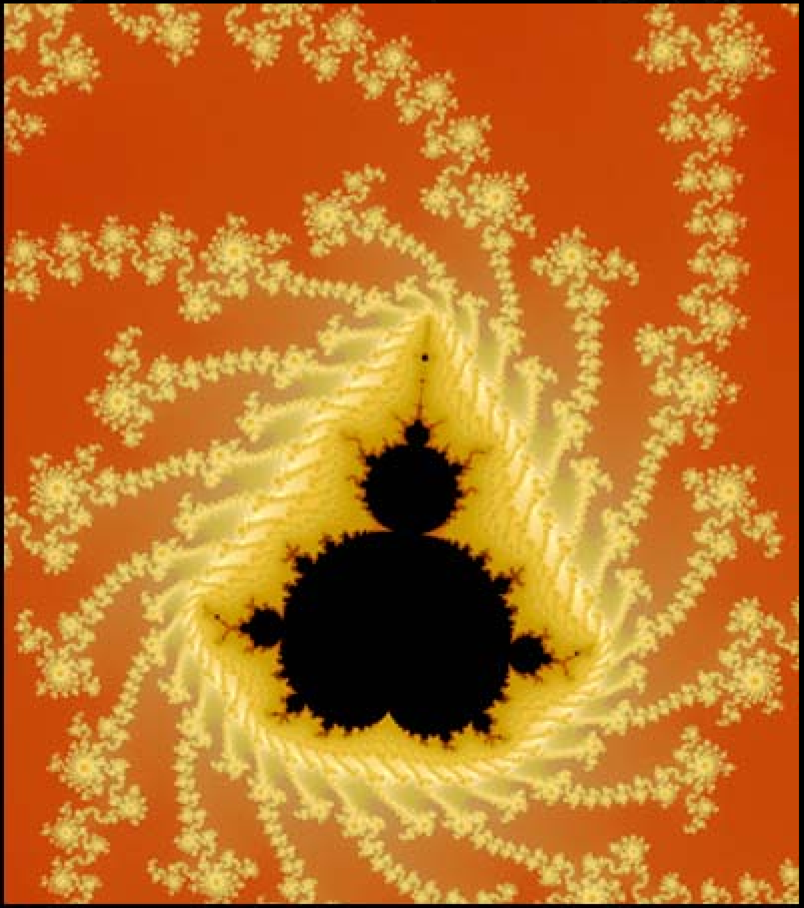
On Compressibility

The Mandelbrot set despite it’s complex nature is actually extremely compressible in the sense that an algorithm for the image is far simpler to store than the image itself!

The Mandelbrot Set



The Mandelbrot Set



Mandelbrot Set Fractal Image
with Very Similar Form and Proportions

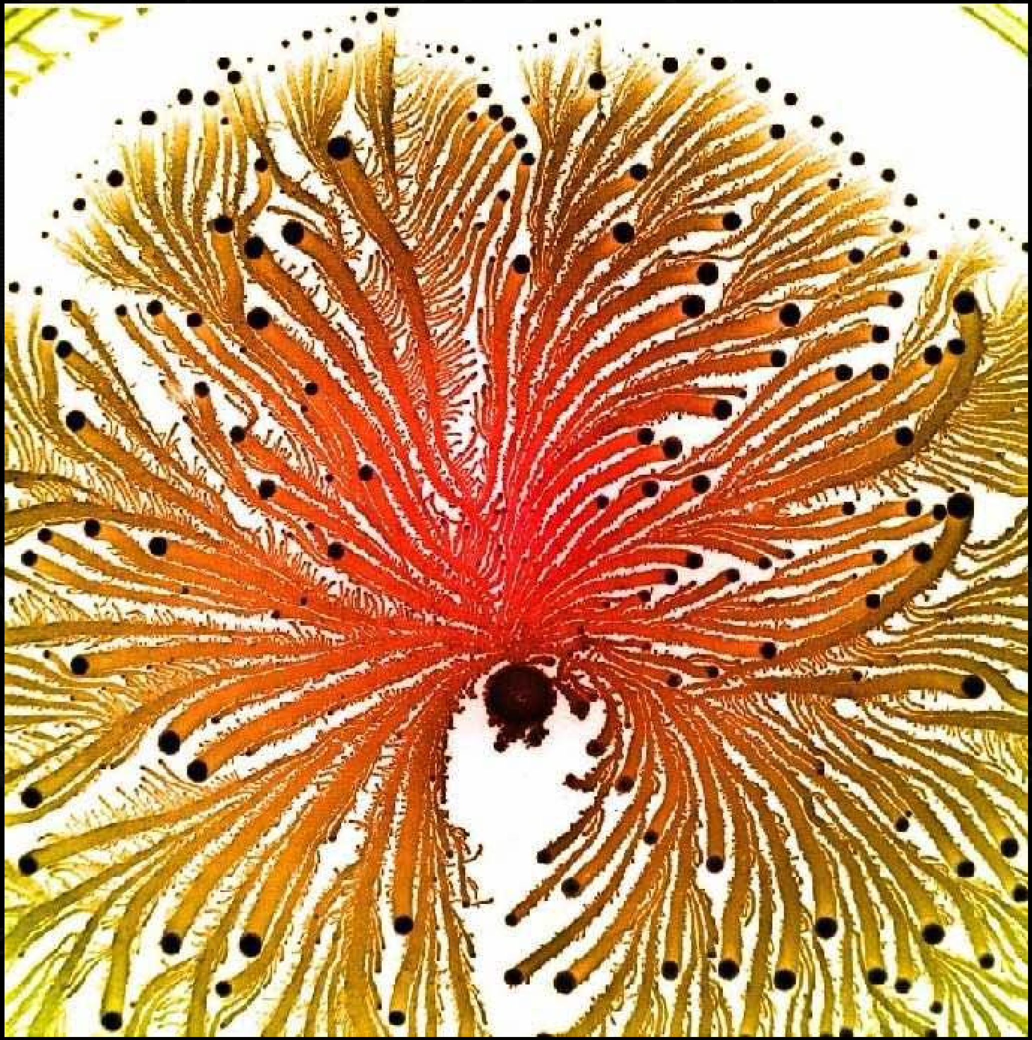
Self-Similarity and Scale-Invariance

Diffusion-Limited Aggregation

Is this a living organism?

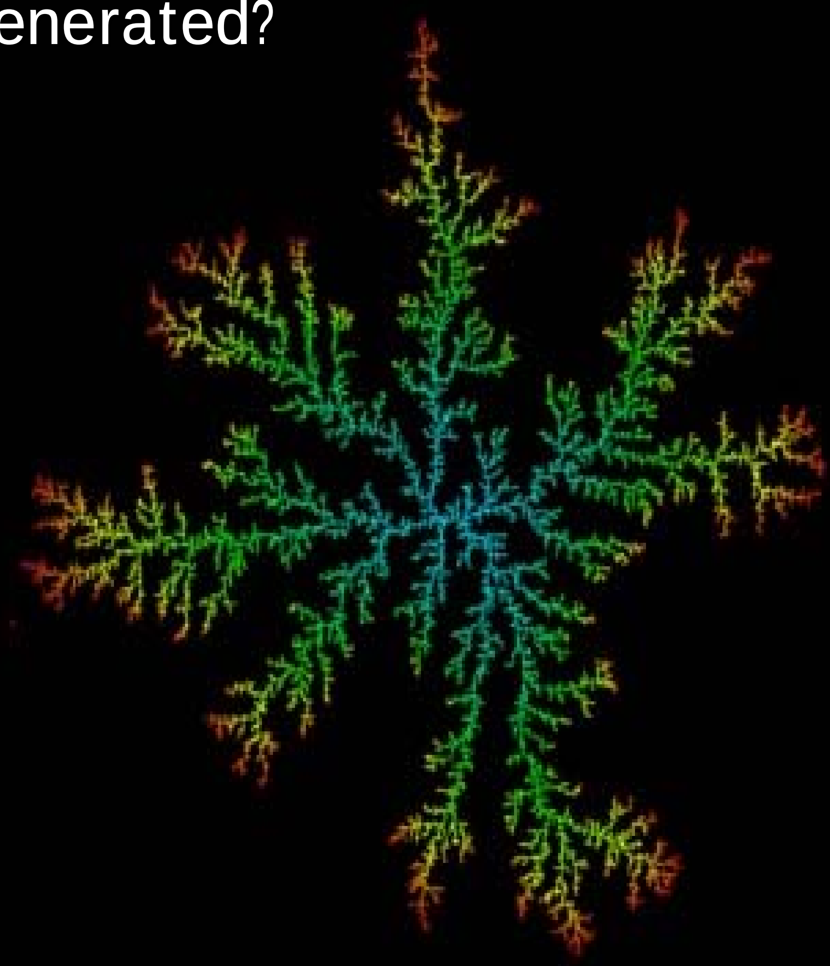
Diffusion-Limited Aggregation

What about this one?



Diffusion-Limited Aggregation

How was this pattern generated?



A DLA pattern (Witten and Sander)

Diffusion-Limited Aggregation

Two processes:

- Diffusion
- Aggregation

Diffusion (Random Walk)

- Diffusion is a random motion
- Although the motion of individual particles is totally random with respect to the direction, it may happen that particles walk somewhat far relative to a starting point
- But, in contrary to a normal flow, where all particles under investigation move more or less into the same direction, <u>the average of walked distance of all particles within a random walk is zero</u>

Aggregation

- When particles have the possibility to attract each other and stick together, they may form *aggregates*
- The forces between the particles may be weak or strong
- For particles which carry some electrical charge (ions) the forces are typically very strong and thus there is a gain in energy when they build aggregates

Diffusion-Limited Aggregation

- In diffusion-limited aggregates the shape of the structure is controlled by the possibility of particles to reach the aggregate
- Starting with a uniform distribution, and some ‘seed’ particles which start the growth process
- The rate of growth is governed/limited by the diffusion
- Some particles might meet, and the aggregate may grow as long there are particles moving around
- Preferential attachment at tip of branches
- The volume is not filled in its entirety, but there are many gaps → Fractality!
- Found in crystal growth, coral reefs, bacterial colonies, and other natural systems

Diffusion-Limited Aggregation

http://apricot.ap.polyu.edu.hk/~lam/dla/dla.html

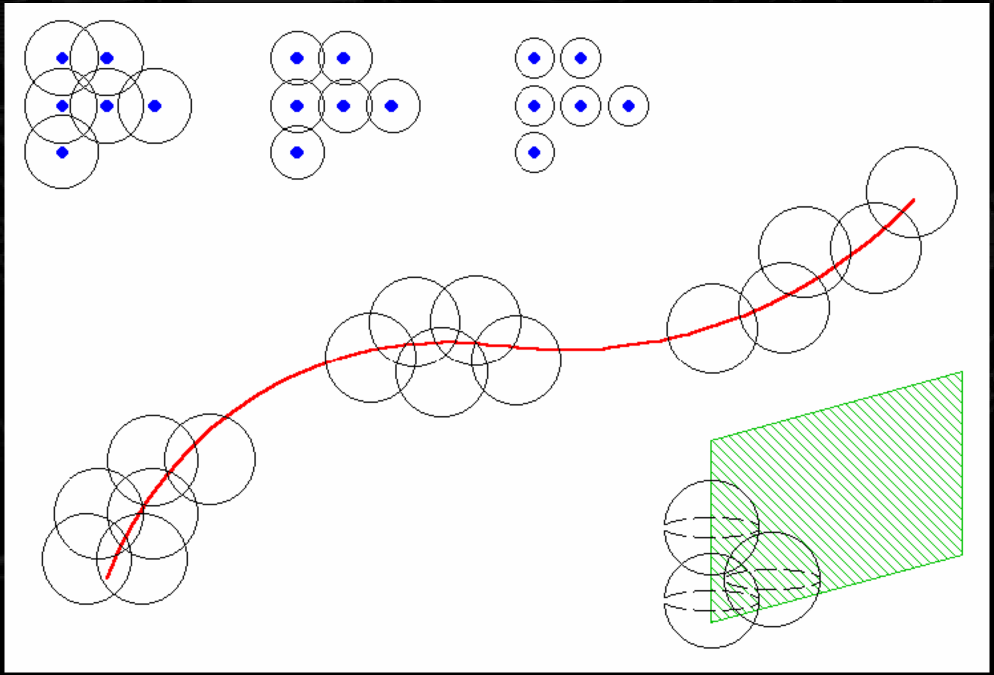
How Do We Measure Self-Similarity and Scaling?

Dimension

- A quantitative measure of self-similarity and scaling
- Intuitively: The dimension tells us how many pieces we see when we look at a finer resolution.
- Definitions:
  - Topological dimension (always integer)
  - Self-similarity dimension (fractal)
  - Capacity dimension (fractal)
  - Hausdorff dimension
  - Embedding dimension

Topological Dimension

- Always an integer (not fractal!)
- in a minimal covering, each point of the object is covered by no more than G sets
- Topological dimension d = G-1
- For a plane: G = 3 → d = 3-1 = 2



Self-Similarity Dimension

Simplest fractals are self-similar!

How many times does scaled-down copy fit into the whole object?

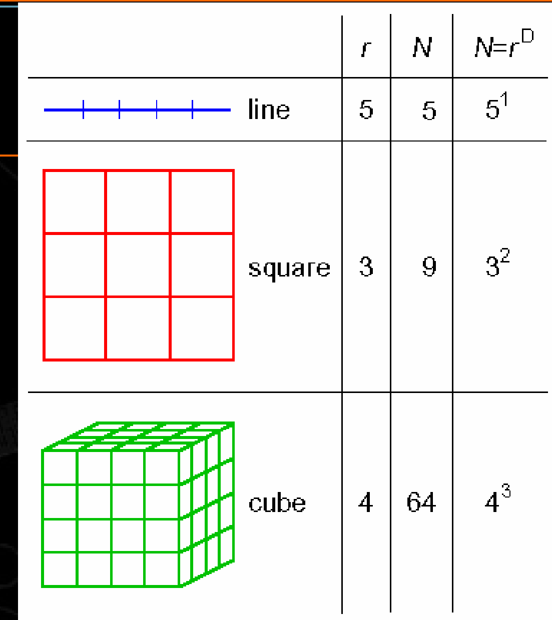
N = number of copies

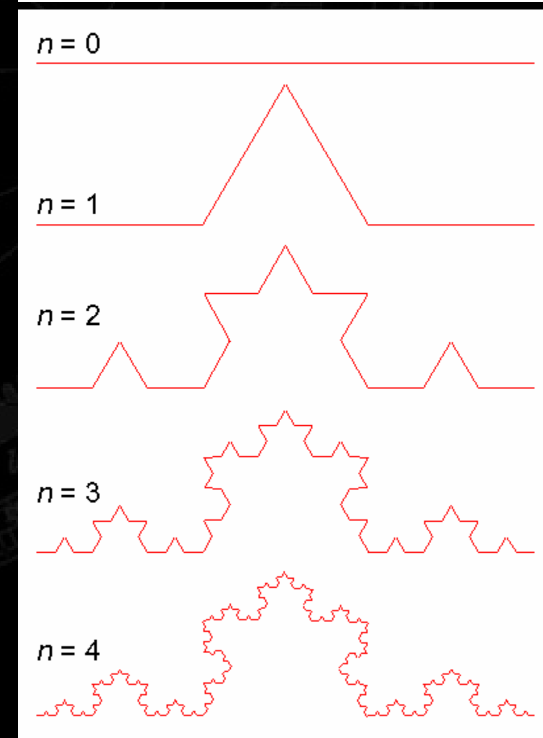
r = scale factor

Self-similarity dimension = ln(N)/ln(r)

E.g. square: N = 9, r = 3 → Ssd = ln(9)/ln(3) = 2

What is the self-similarity dimension of the Koch curve?





Fractal Dimension: Koch Curve

$$D = \frac{\text{Log (number of new pieces)}}{\text{Log (factor of finer resolution)}}$$

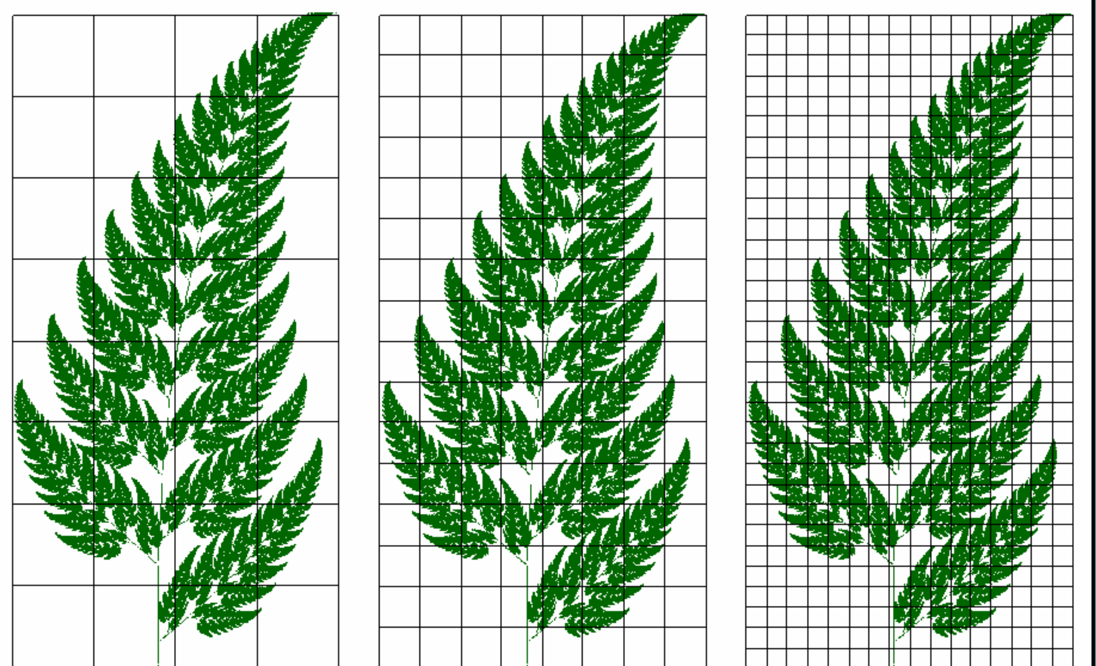
$$= \frac{\text{Log } 4}{\text{Log } 3} = \mathbf{1.2619}$$

Box Dimension

- Used for fractals that are not self-similar
- N (r) balls or squares of radius 1/r needed to cover the object
- Box dimension

$$d = \lim_{r \to 0} \frac{\ln N(r)}{\ln r}$$

- D = 1.65 (?)



Definition of a Fractal

Mathematical:

d(fractal) > d(topological)

Origin:

Fractal = fragmented, many pieces, one also speaks of fractal dimension

Example: Koch Curve

Perimeter:

d(fractal) = 1.2619

d(topological) = 1.

In other words: Perimeter covers more space than a 1-D line; covers less space than a 2-D area.

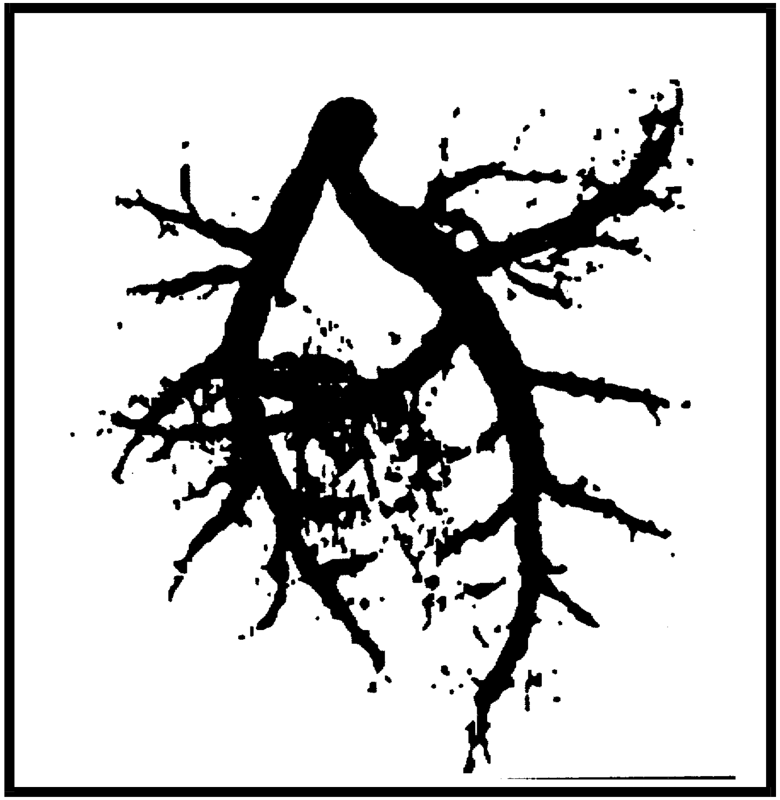
Fractal Dimensions in Biology: Measured

- surfaces of proteins
- surface of cell membranes
- growth of bacterial colonies
- islands of types of lipids in cell membranes
- dendrites of neurons
- blood flow in the heart
- blood vessels in the eye, heart, and lung
- shape of herpes simplex
- ulcers in the cornea
- textures of X-rays of bone and teeth
- texture of radioisotope tracer in the liver
- MANY MORE!

Pulmonary Hypertension

HIGH BLOOD PRESSURE IN THE LUNGS

Boxt, Katz, Czegledy, Liebovitch, Jones, Reid, & Esser
1990 Circ. Suppl, III, 82: 100



$\boxed{D = 1.65}$

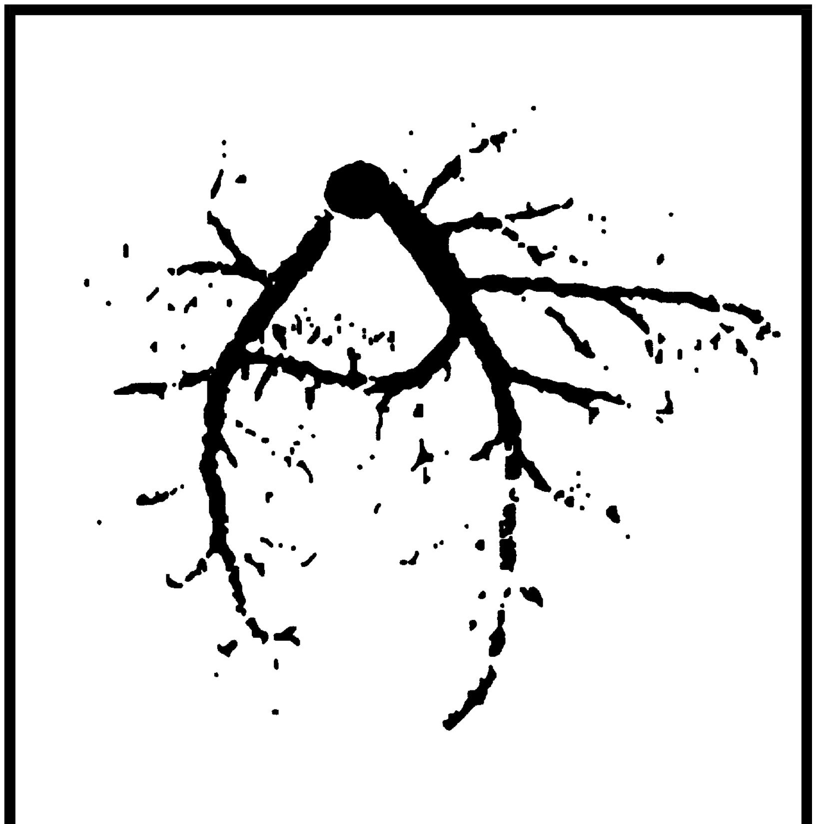
normal

20% 0_2

Pulmonary Hypertension

HIGH BLOOD PRESSURE IN THE LUNGS

Boxt, Katz, Czegledy, Liebovitch, Jones, Reid, & Esser
1990 Circ. Suppl, lll, 82: 100



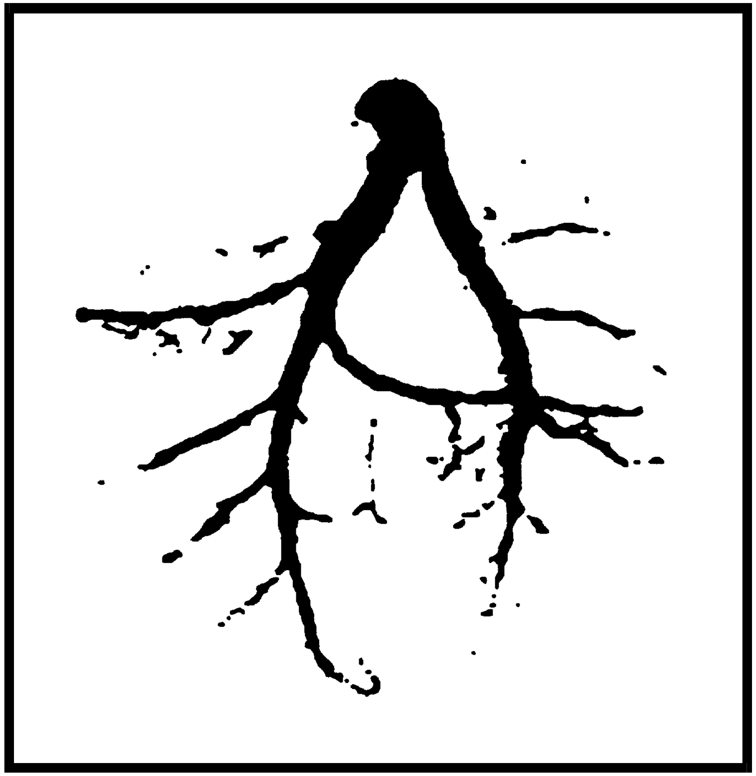
$\boxed{D = 1.53}$

hypoxic
10% 0_2

Pulmonary Hypertension

HIGH BLOOD PRESSURE IN THE LUNGS

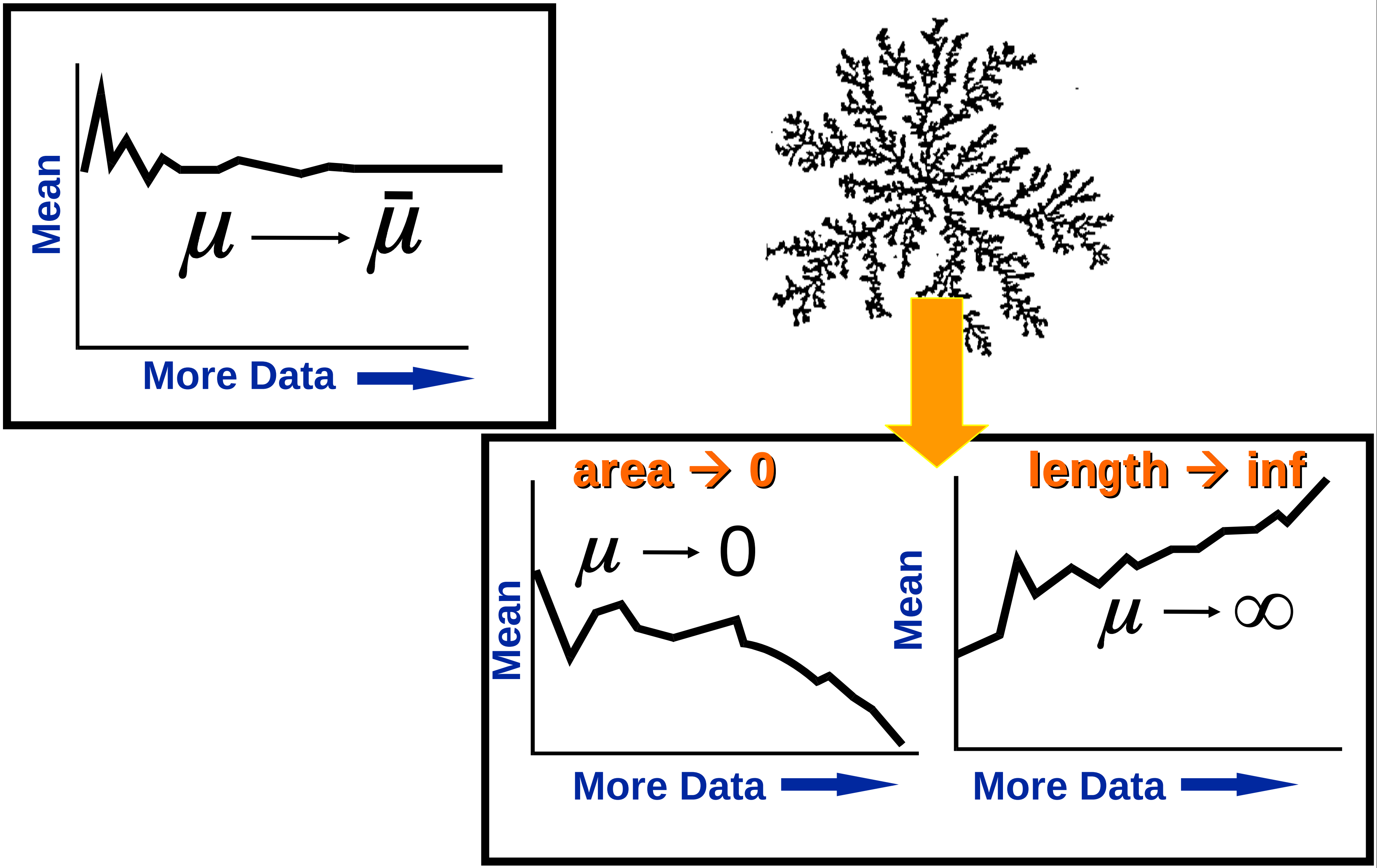
Boxt, Katz, Czegledy, Liebovitch, Jones, Reid, & Esser
1990 Circ. Suppl, lll, 82: 100



$\boxed{D = 1.43}$

hyperoxic
90% 0_2

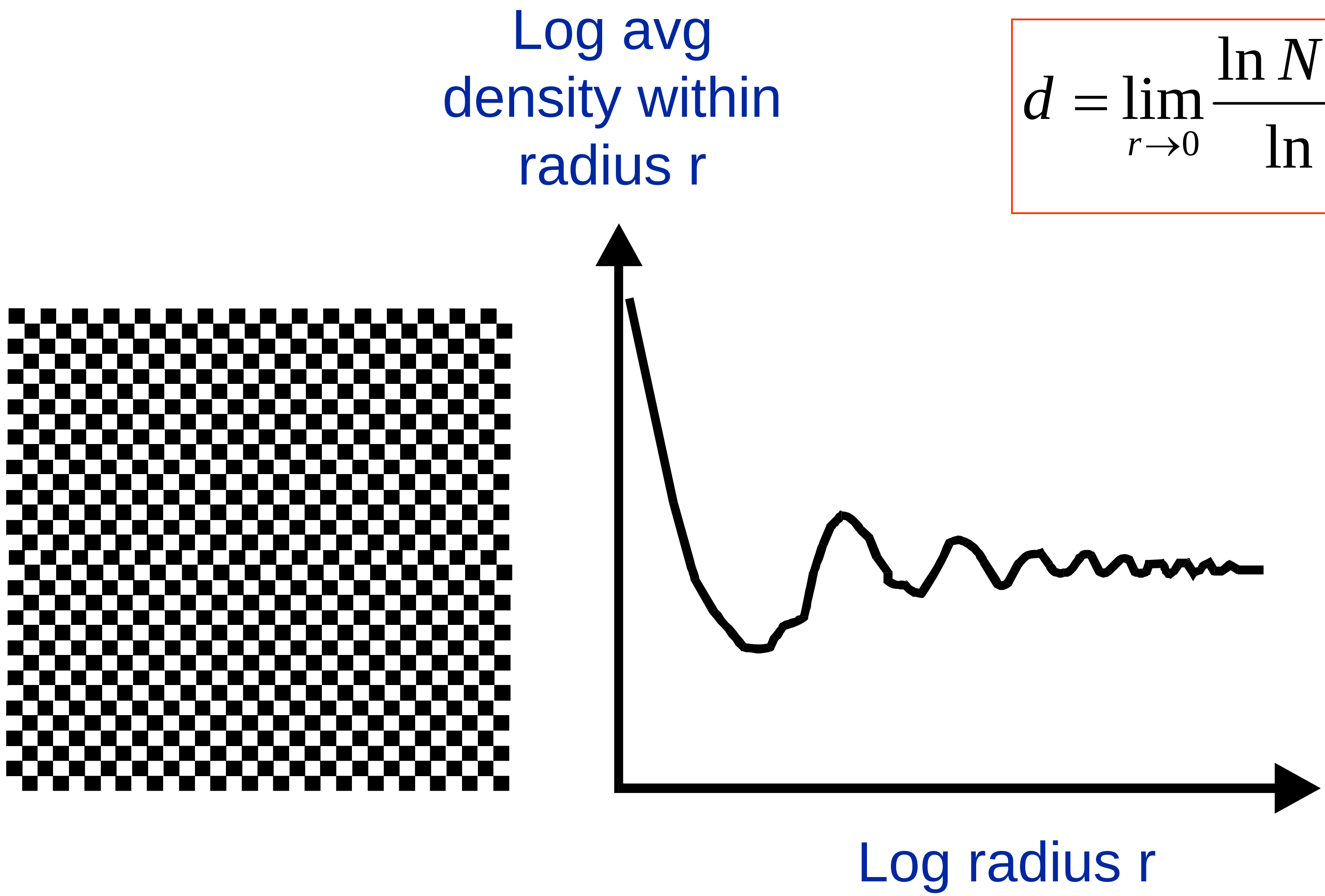
Statistical Indicators of Fractal Structure



Statistical Indicators of Fractal Structure

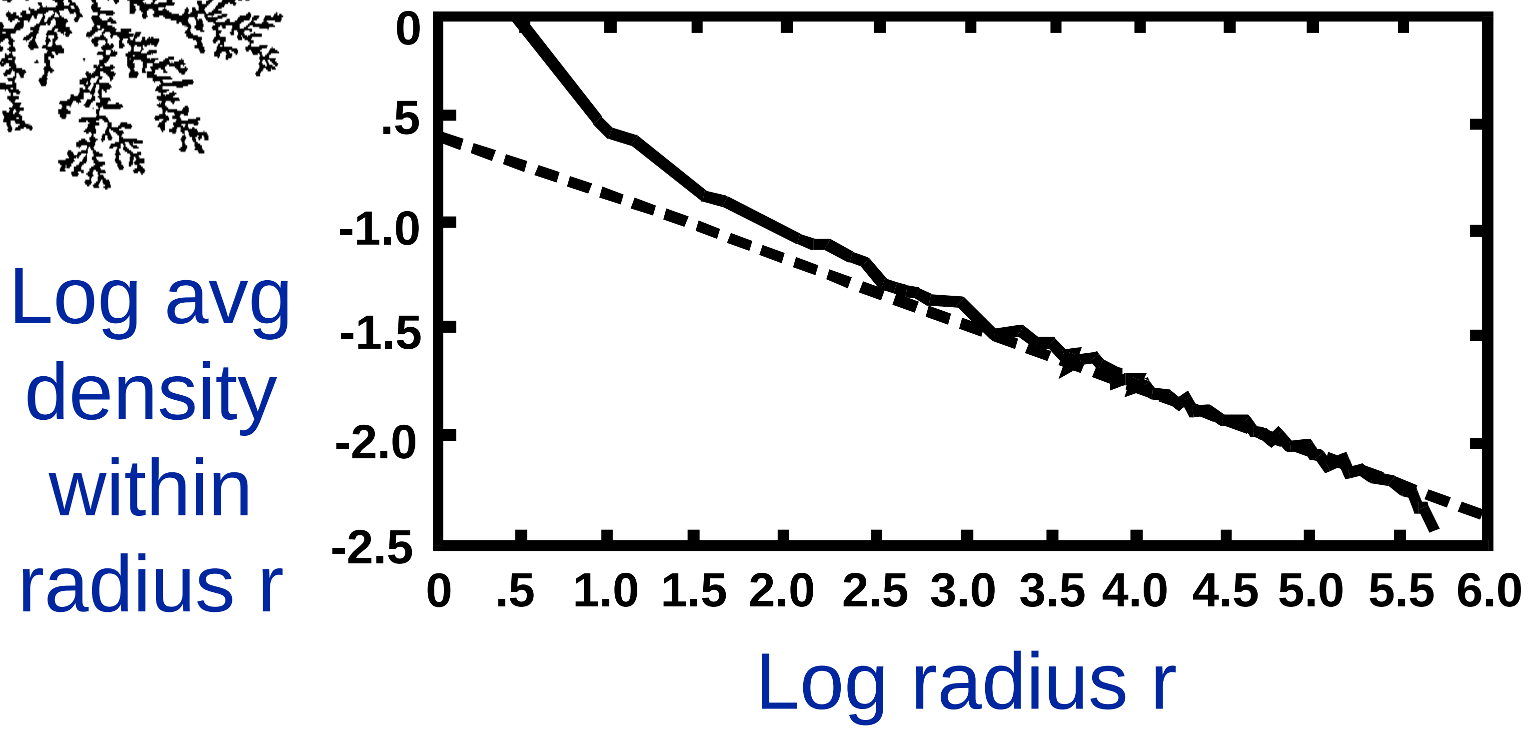
Remember!

$$d = \lim_{r \to 0} \frac{\ln N(r)}{\ln r}$$

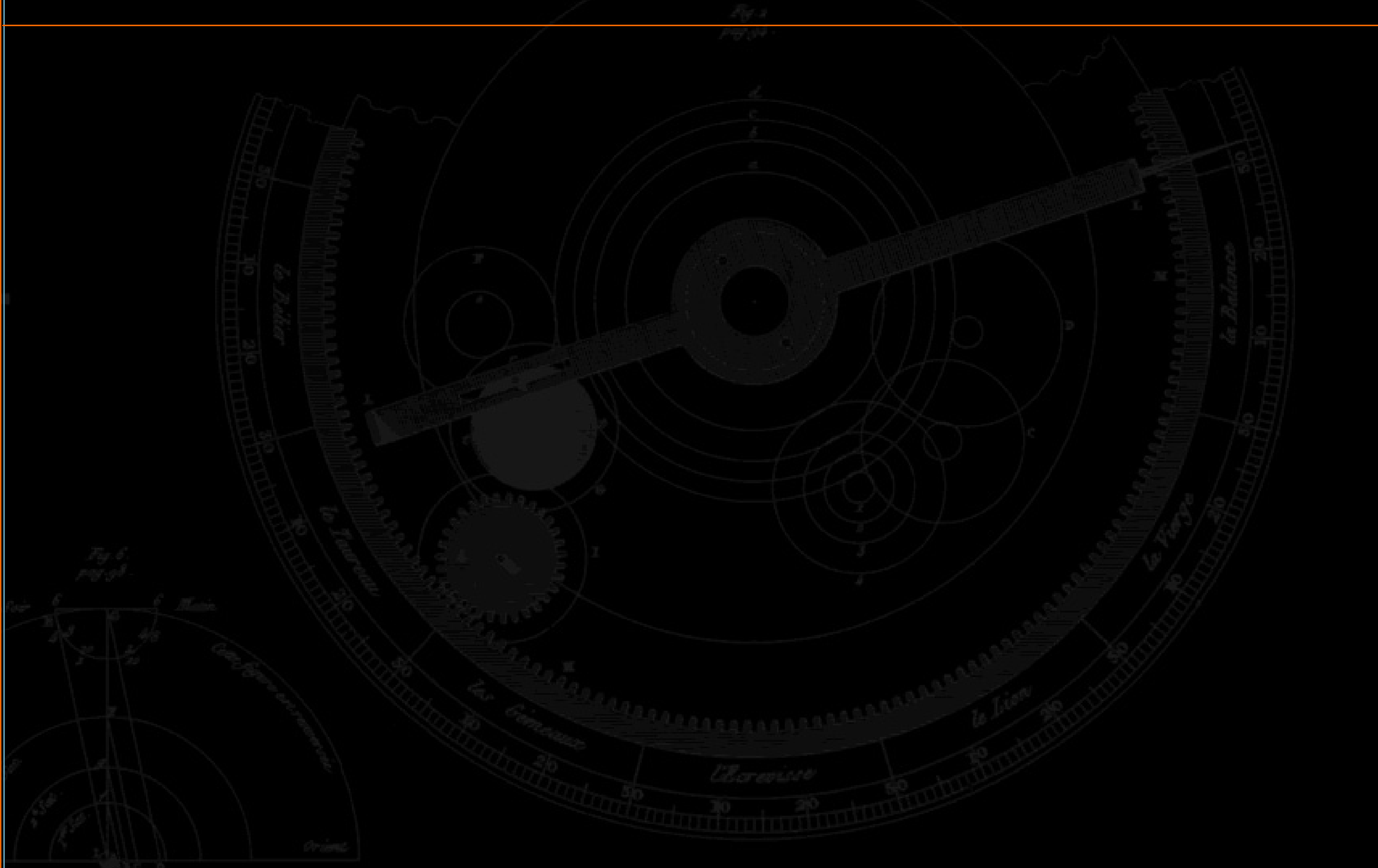


Statistical Indicators of Fractal Structure

Meakin 1986 In *On Growthand Form: Fractal and Non-Fractal Patterns in Physics* Ed. Stanley & Ostrowsky, Martinus Nijoff Pub., pp. 111-135

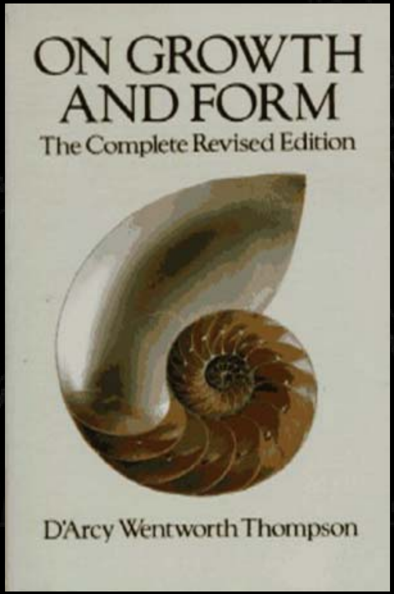


Natural Design Principles



Mathematics: the Language of Nature

On Growth and Form



On Growth and Form (1917) laid the foundations of <u>bio-mathematics</u>

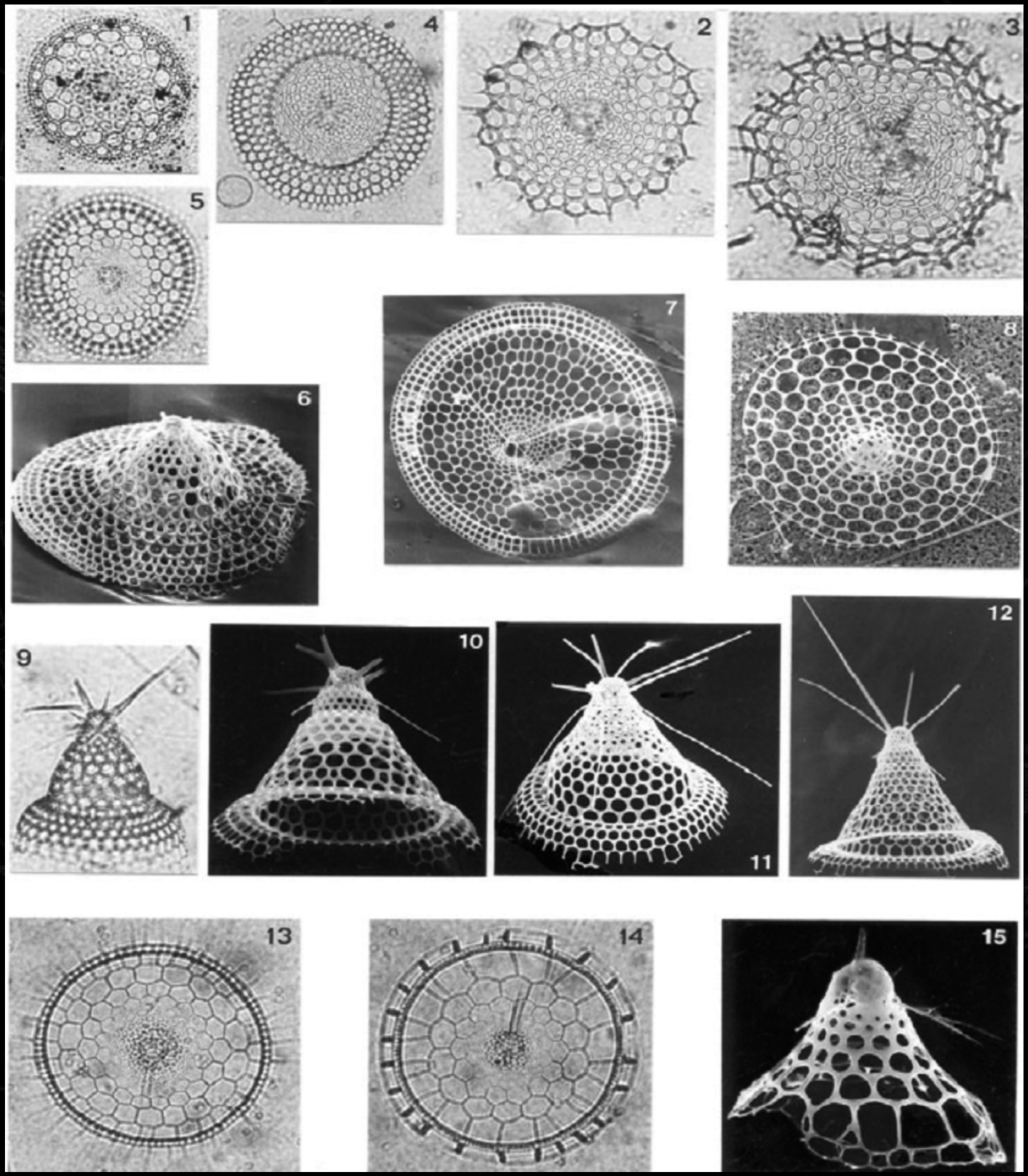
"Organic form itself is found, mathematically speaking, to be a function of time [...] We might call the form of an organism an event in space-time, and not merely a configuration in space."

Eqs. to describe static patterns of living organisms

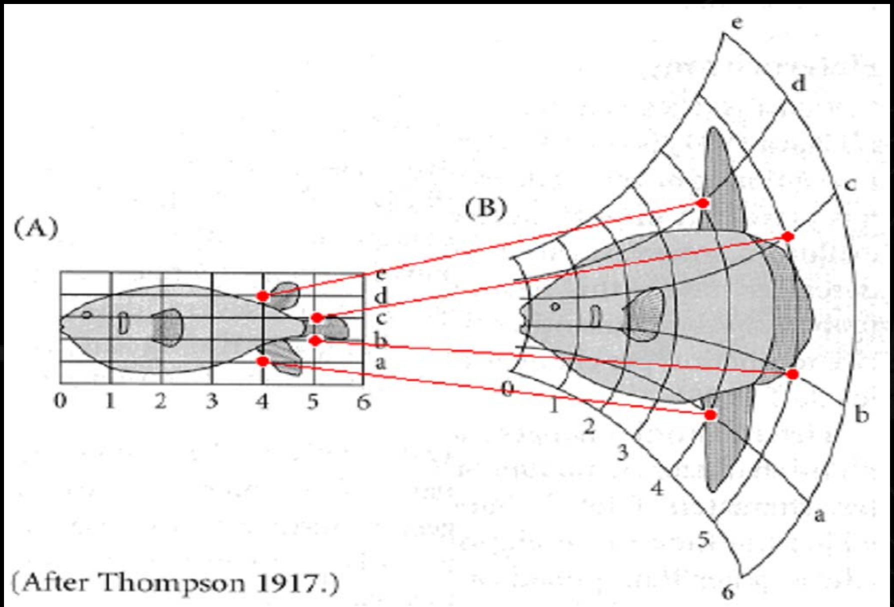
Transforming form changing a few parameters

"In many growth processes of living organism, especially of plants, regularly repeated appearances of certain multicellular structures are readily noticeable [...] In the case of a compound lead, for instance, some of the leaflets which are parts of a leaf at an advanced stage, have the same shape as the whole leave has at an earlier stage." (Herman et al.)

On Growth and Form

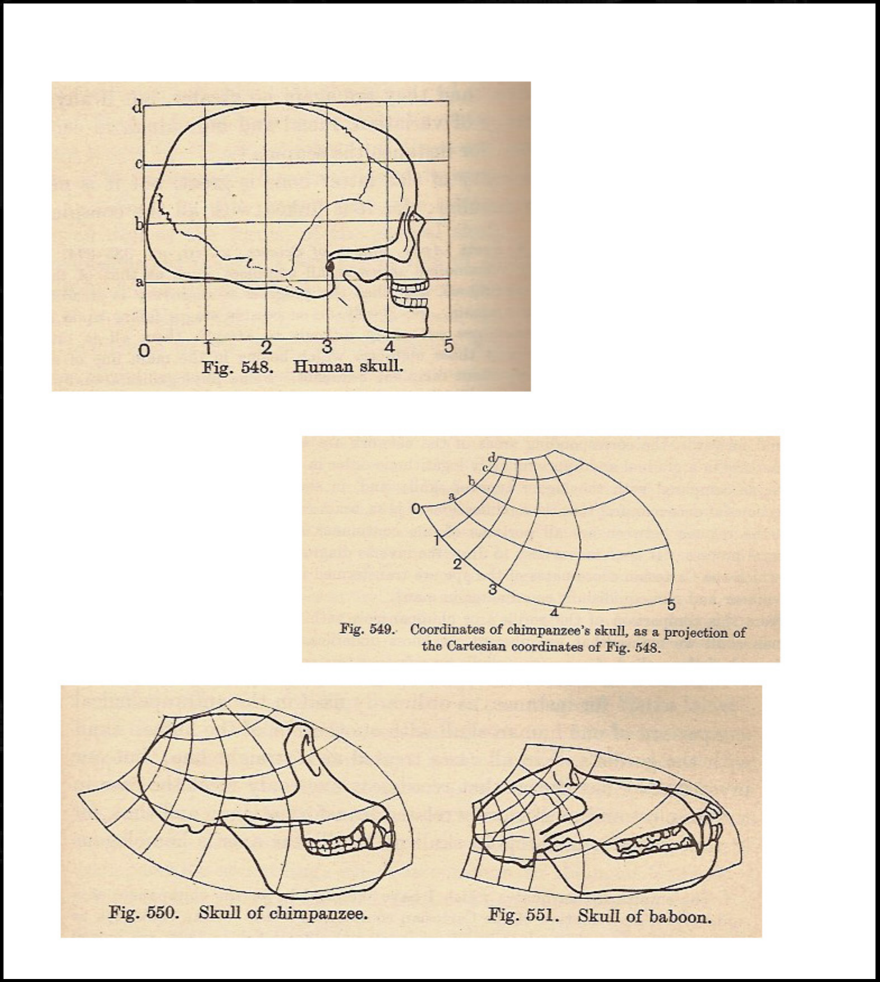


Affine Transformations

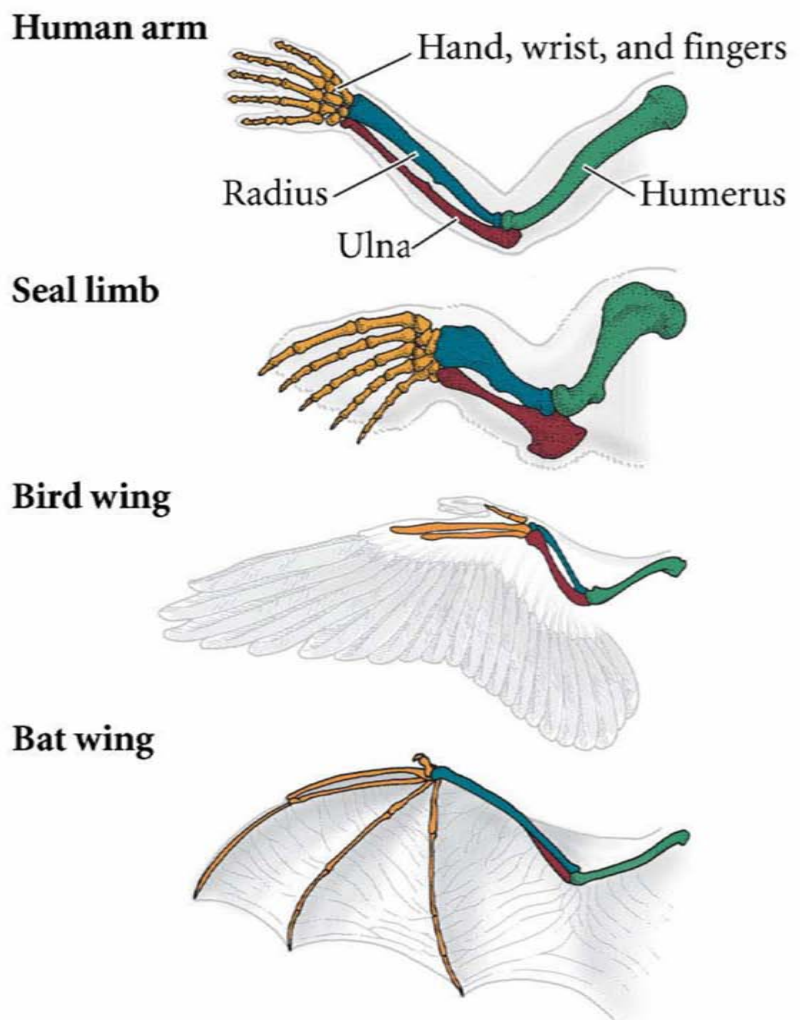


Theory of transformation:

Comparison of related morphological forms (Thompson, 1917)



Homology of Structure



DEVELOPMENTAL BIOLOGY, Eighth Edition, Figure 1.13

On Growth

Three mechanisms:

- Iteration
- Recursion
- Diffusion

On Growth and Form: L-Systems

- The self-similarity of plants is the result of developmental processes
- Mathematical formalism introduced in 1968 by Aristid Lindenmeyer (1925-1989)
- Essentially, production system
- Productions are rewriting rules which state how new symbols (or cells) can be produced from old symbols (or cells)

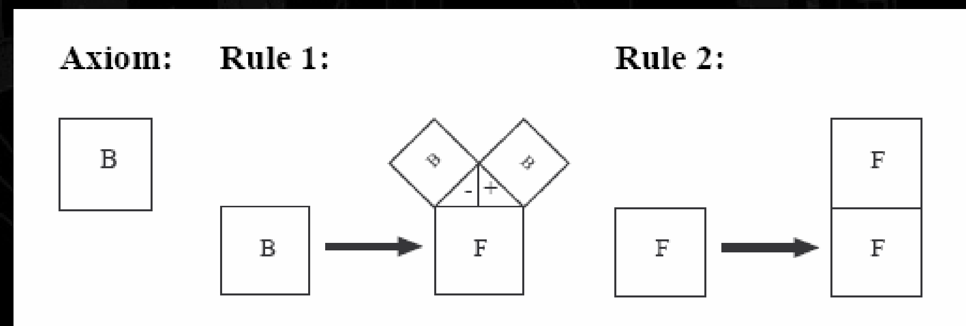
Example

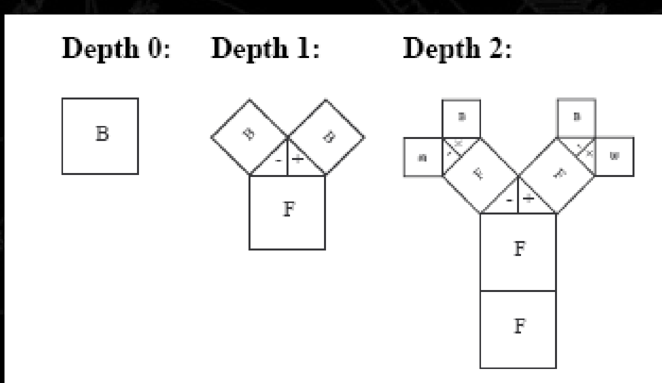
Axiom: B

Rule 1: $B \rightarrow F[-B] + B$

Rule 2: $F \rightarrow FF$

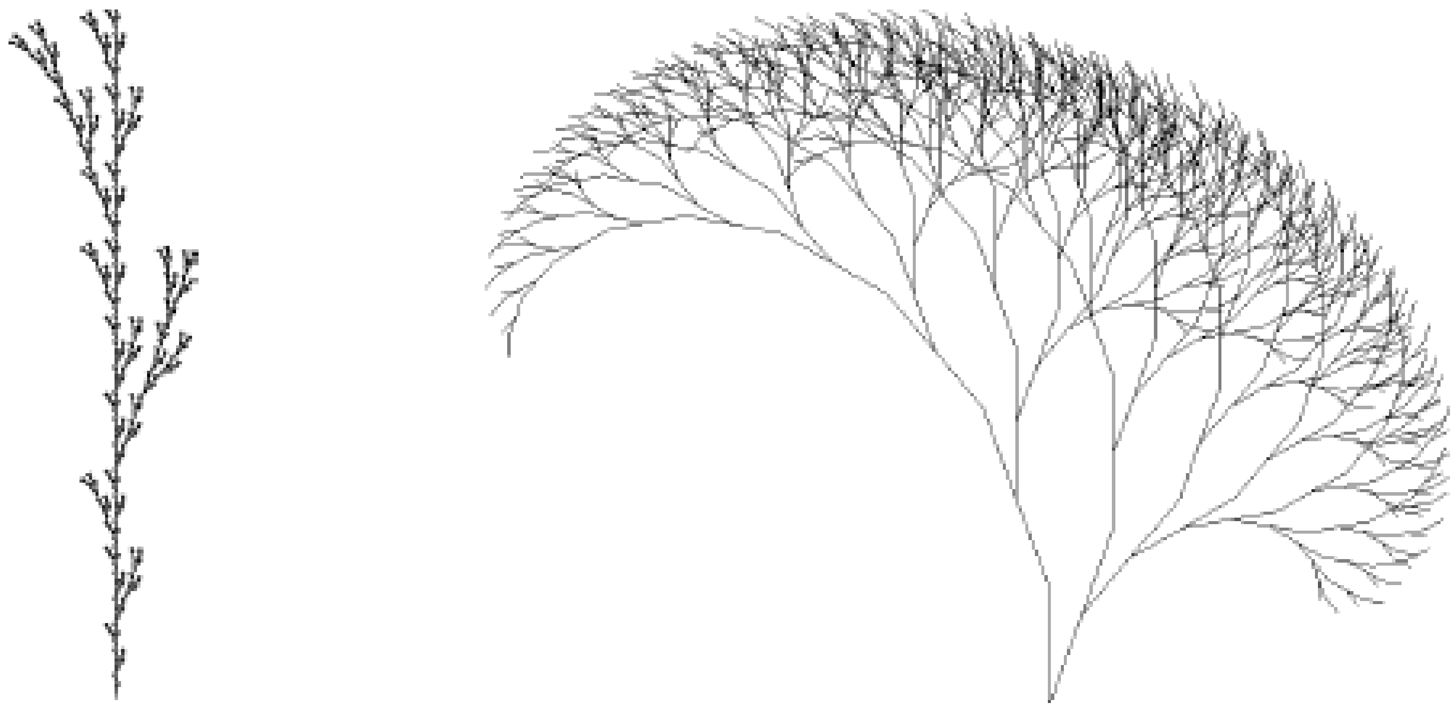
- Axiom = seed ‘cell’
- Rule = description of how to grow new ‘cell’





F = draw forward
G = go forward (but do not draw)
+ = right turn
- = left turn
[= save turtle’s current pos
] = remove last saved pos

L-Systems



Axiom: *F*
Rule: *F = F [-F] F [+F] F*
Angle: 20
Depth: 7

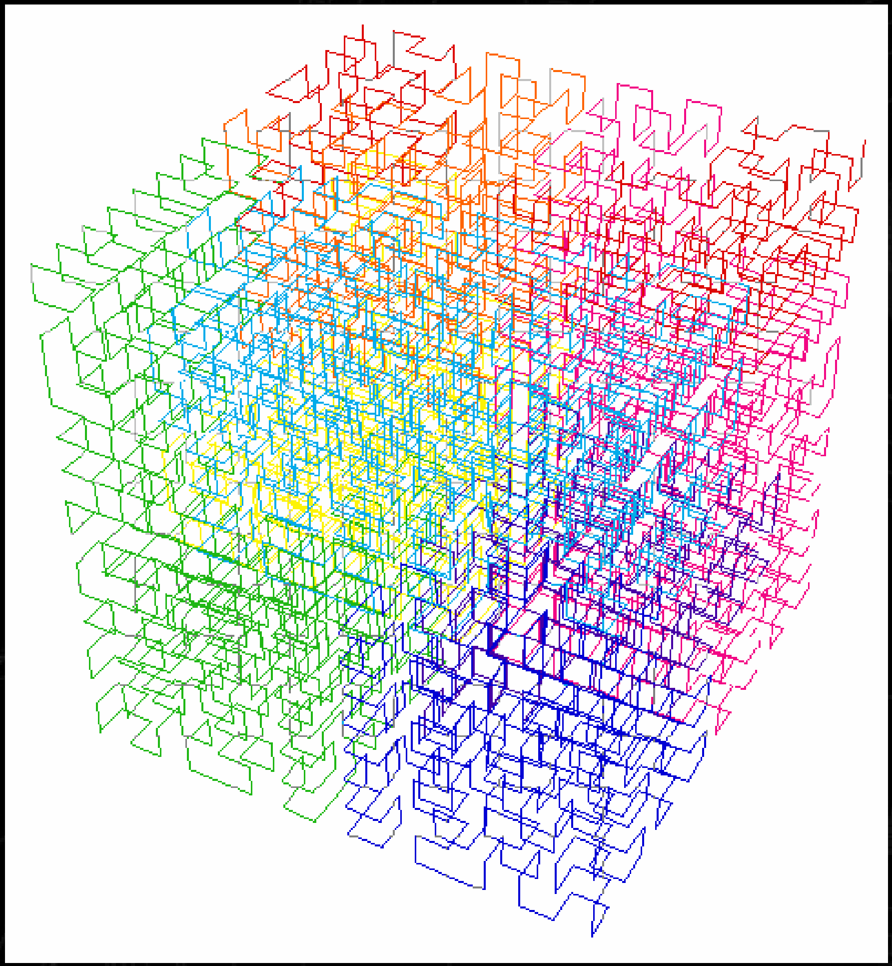
Axiom: *F*
Rule: *F = | [+F] | [-F] +F*
Angle: 20
Depth: 9

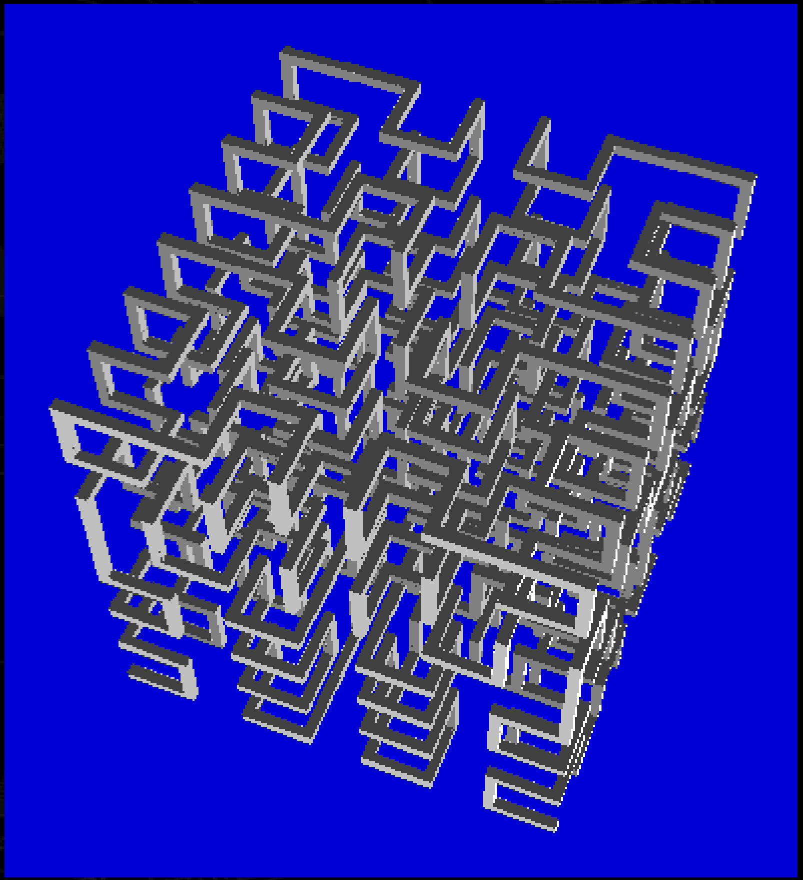
Figure 2.13: *A few examples of L-systems (from Flake, 1998).*

More sophisticated L-Systems

00:22:50

Three-Dimensional L-Systems

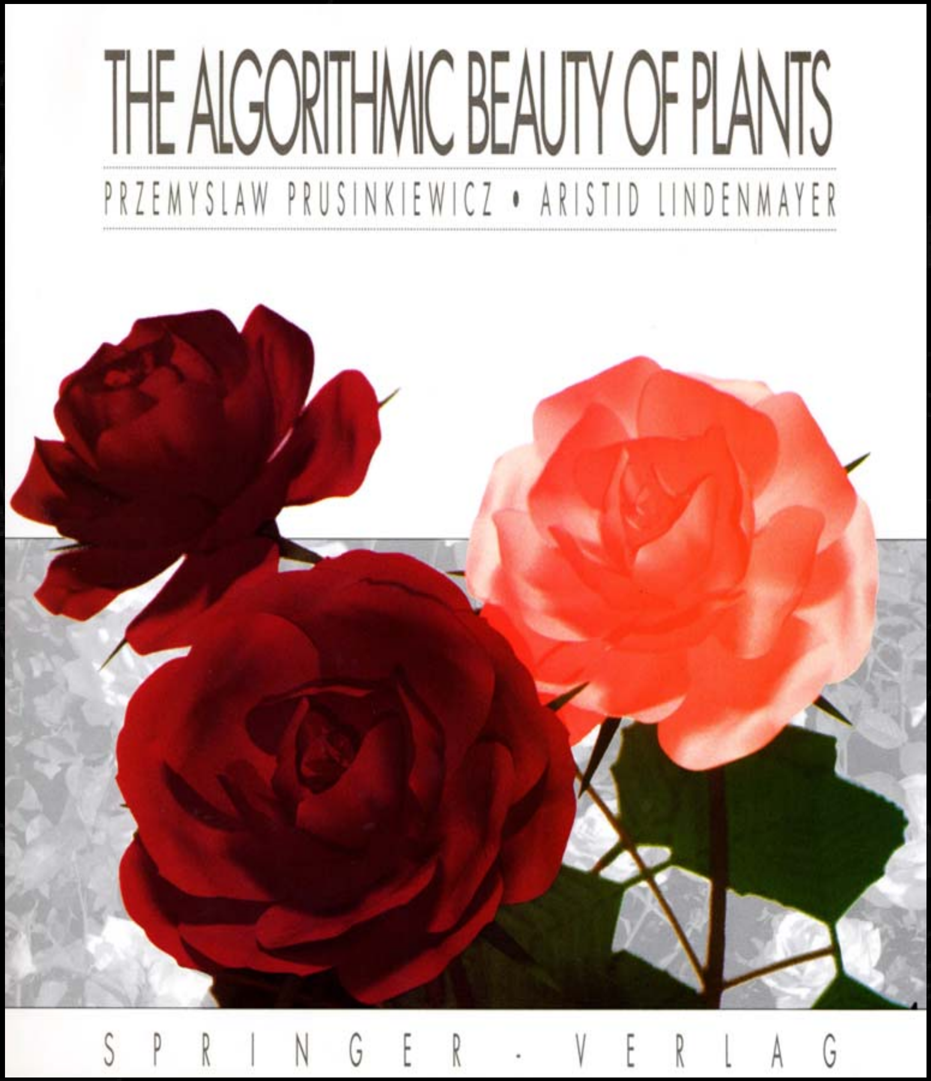




Movies

...

Book



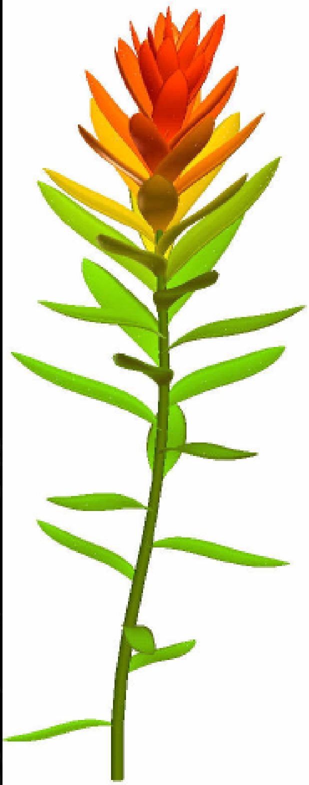
Available for free online!

Project Idea

Plant Modeling

with

CPFG | Virtual Laboratory | L-studio



CPFG is a plant simulation program based on the formalism of Lindenmayer systems (L-systems). Its distinctive feature is the flexible modeling language that allows the user to specify the architecture of various modular organisms, from filamentous bacteria and algae to herbaceous plants, trees, and plant ecosystems.

The models can be descriptive or mechanistic (functional-structural) in nature. In the latter case, the user can investigate the impact of physiological (endogenous) and environmental (exogenous) processes on plant development. The results of simulations are visualized as diagrammatic or realistic images of plants. Numerical results are output in user-defined formats as needed for further mathematical analysis.

http://algorithmicbotany.org/virtual_laboratory/

L-Systems

Needless to say … L-Systems display fractal structure ☺

On Growth and Form: Morphogenesis

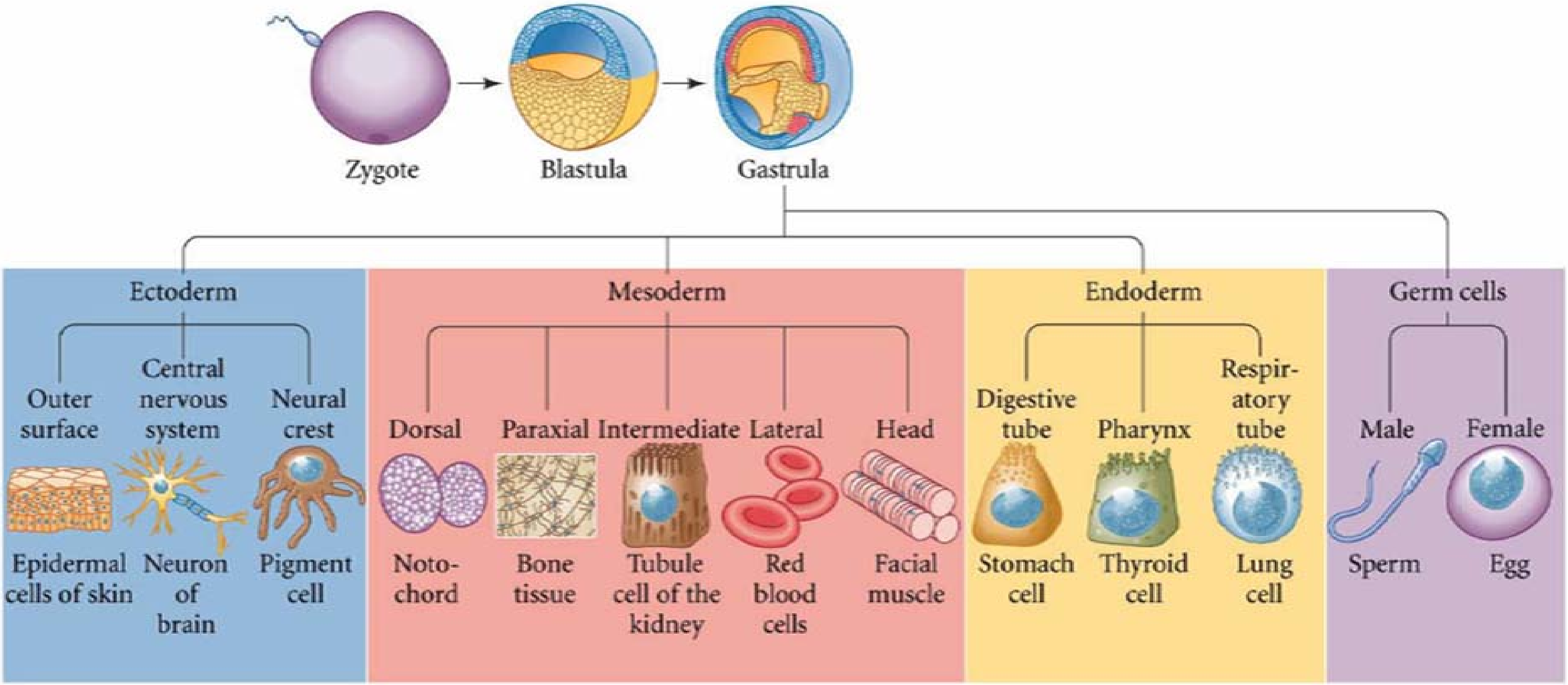
Morphogenesis = morphology (shape, form) + genesis (development)

Technically speaking: stage in embryonic development

Cells begin to cluster and form patterns:

- Cell differentiation
- Cell growth
- Cell division
- Cell migration
- Chemical secretion/diffusion ...

Cell Differentiation: Vertebrates



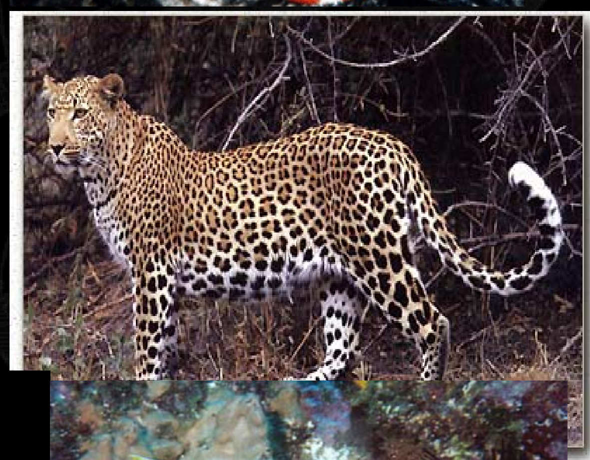
DEVELOPMENTAL BIOLOGY, Eighth Edition, Figure 1.1 © 2006 Sinauer Associates, Inc.

- Three stages
- Four cell types

On Growth and Form: Morphogenesis

- How does body structure arise?
- If arm cells had an extra cycle of cell division, our arms would be 1.8m long … how is growth controlled?
- How is cell division turned on or off? The early embryo is like a cancerous tumor – growing very rapidly – but the embryo “knows” when to stop growing and diving.
- What are the <u>mechanisms that determine the anatomical structure of an organism</u>?

Striped Patterns and Spotted Bodies



Morphogenetic Model

[Classic] "The Chemical Basis of Morphogenesis," 1952, *Phil. Trans. Roy. Soc. of London*, **Series B: Biological Sciences,** *237*:**37—72.**

THE CHEMICAL BASIS OF MORPHOGENESIS

By A. M. TURING, F.R.S. *University of Manchester*

(*Received* 9 *November* 1951—*Revised* 15 *March* 1952)

It is suggested that a system of chemical substances, called morphogens, reacting together and diffusing through a tissue, is adequate to account for the main phenomena of morphogenesis. Such a system, although it may originally be quite homogeneous, may later develop a pattern or structure due to an instability of the homogeneous equilibrium, which is triggered off by random disturbances. Such reaction-diffusion systems are considered in some detail in the case of an isolated ring of cells, a mathematically convenient, though biologically unusual system. The investigation is chiefly concerned with the onset of instability. It is found that there are six essentially different forms which this may take. In the most interesting form stationary waves appear on the ring. It is suggested that this might account, for instance, for the tentacle patterns on *Hydra* and for whorled leaves. A system of reactions and diffusion on a sphere is also considered. Such a system appears to account for gastrulation. Another reaction system in two dimensions gives rise to patterns reminiscent of dappling. It is also suggested that stationary waves in two dimensions could account for the phenomena of phyllotaxis.

The purpose of this paper is to discuss a possible mechanism by which the genes of a zygote may determine the anatomical structure of the resulting organism. The theory does not make any new hypotheses; it merely suggests that certain well-known physical laws are sufficient to account for many of the facts. The full understanding of the paper requires a good knowledge of mathematics, some biology, and some elementary chemistry. Since readers cannot be expected to be experts in all of these subjects, a number of elementary facts are explained, which can be found in text-books, but whose omission would make the paper difficult reading.

Reaction-Diffusion Systems

Key idea: Morphology is the result of two substances ‘a’ and ‘b’ (morphogens) diffusing at different rates

Morphogen: “is simply the kind of substance concerned in this theory…” in fact, anything that diffuses into the tissue and “somehow persuades it to develop along different lines from those which would have been followed in its absence” qualifies. (Generator of form)

- Investigation of pattern due to breakdown of symmetry and homogeneity in initially homogeneous continuous media
- Breakdown captured by set of differential equations
- Equations capture dynamics of autocatalytic and antagonistic chemical reactions with diffusion
- Result = Turing patterns

Pattern Formation from Homogenous I.C.

Activator-Inhibitor Model

Requirements:

- Activator: local self-enhancement (positive feedback)
- Inhibitor: Long-range antagonistic effect (negative feedback)
- Diffusion: Diffusion of inhibitor >> diffusion of activator (>7 times faster) → inhibitor must act rapidly (rapid adaptation of inhibitor concentration) – otherwise oscillations will occur
- Decay (removal): Decay inhibitor > decay activator

Pattern formation:

- Small deviations from a homogeneous distribution create a strong positive feedback which causes deviations to grow even more.
- A long-range antagonistic effect restricts the self-enhancing reaction and causes a localization.

Activator-Inhibitor Scheme

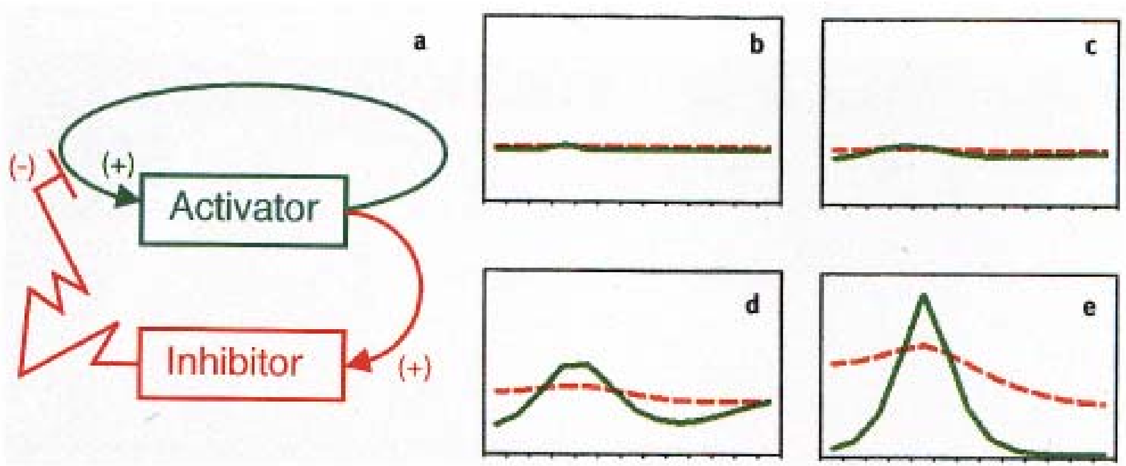


Figure 2.22: Reaction scheme for pattern formation by autocatalysis and long-range inhibition. An activator catalyzes its own production and that of its antagonist (the inhibitor). The diffusion constant of the inhibitor must be much higher than that of the activator. A homogenous distribution of both substances is unstable (b) (the x-axis represents position and the y-axis the concentration). A minute local increase of the activator (——) grows further (c, d) until a steady state is reached in which self-activation and inhibition (- - - -) are balanced (from Meinhardt, 1995).

Diffusion: 1-D Case

$$a(x,t)$$

$$\frac{\partial a}{\partial t} = D_a \frac{\partial^2 a}{\partial^2 x}$$

- Constant concentration difference between neighboring cells a(x,t) and a(x+1,t): net exchange of molecules by diffusion is 0
- Linear concentration gradient: net exchange of molecules by diffusion is also 0 (what goes out come in)
- Hence, second derivate!

first temporal derivative: rate

second spatial derivative: flux

Activator-Inhibitor System: Sea Shells

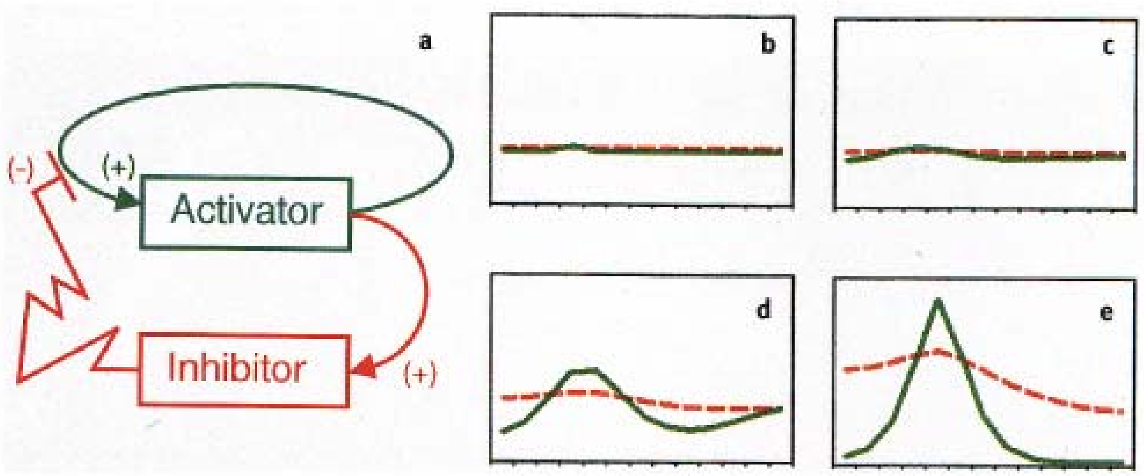


Figure 2.22: Reaction scheme for pattern formation by autocatalysis and long-range inhibition. An activator catalyzes its own production and that of its antagonist (the inhibitor). The diffusion constant of the inhibitor must be much higher than that of the activator. A homogenous distribution of both substances is unstable (b) (the x-axis represents position and the y-axis the concentration). A minute local increase of the activator (——) grows further (c, d) until a steady state is reached in which self-activation and inhibition (- - - -) are balanced (from Meinhardt, 1995).

Activator-Inhibitor System: Sea Shells

$$\frac{\partial a}{\partial t} = s\left(\frac{a^2}{b} + b_a\right) - r_a a + D_a \frac{\partial^2 a}{\partial x^2}$$

$$\frac{\partial b}{\partial t} = sa^2 - r_a b + b_b + D_b \frac{\partial^2 b}{\partial x^2}$$

a(x,t), b(x,t): concentration of activator and inhibitor

s: ability of cells to perform auto-catalysis

Da, Db: diffusion constants

ra, rb: decay rates

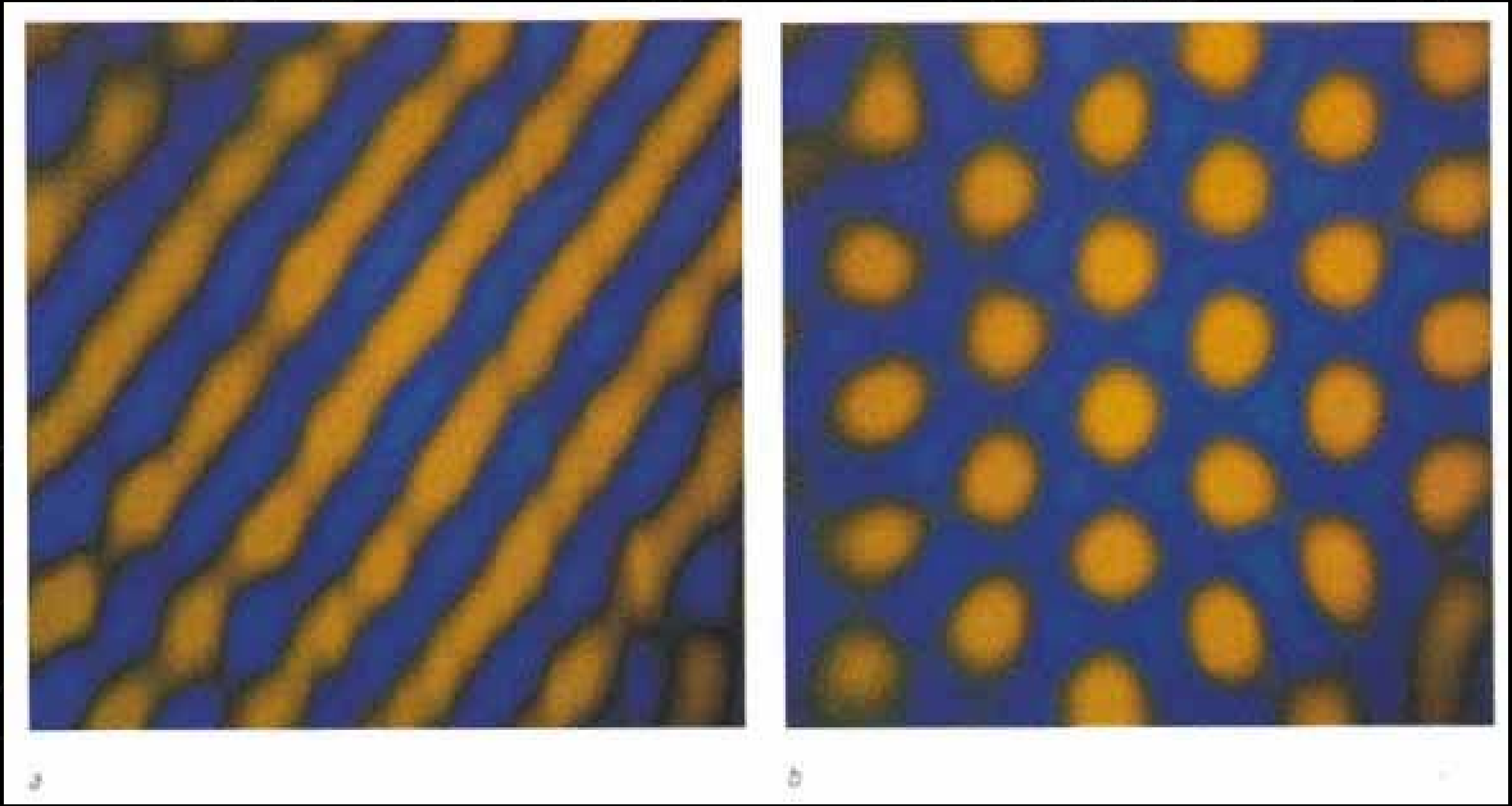
sa^2/b : non-linear autocatalytic influence

$-r_a a$: rate of removal (proportional to concentration)

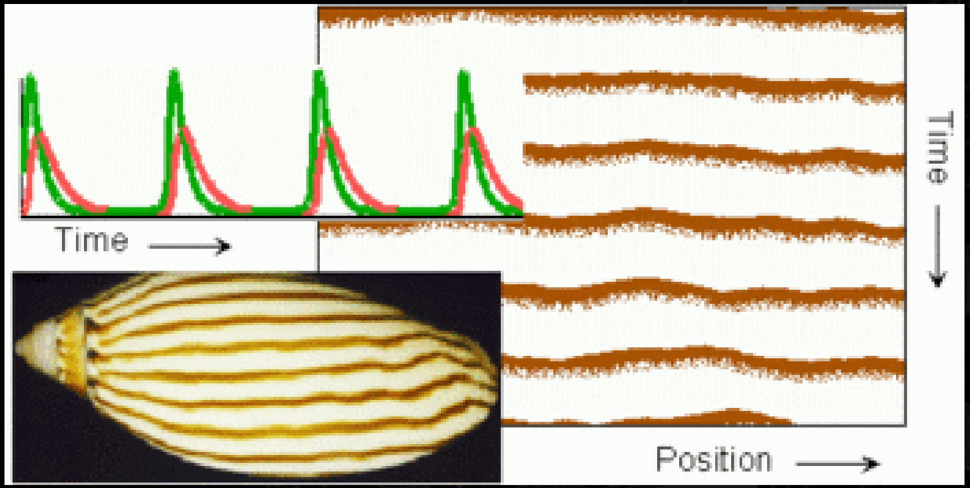
b_a, b_b: basic activator/inhibitor production

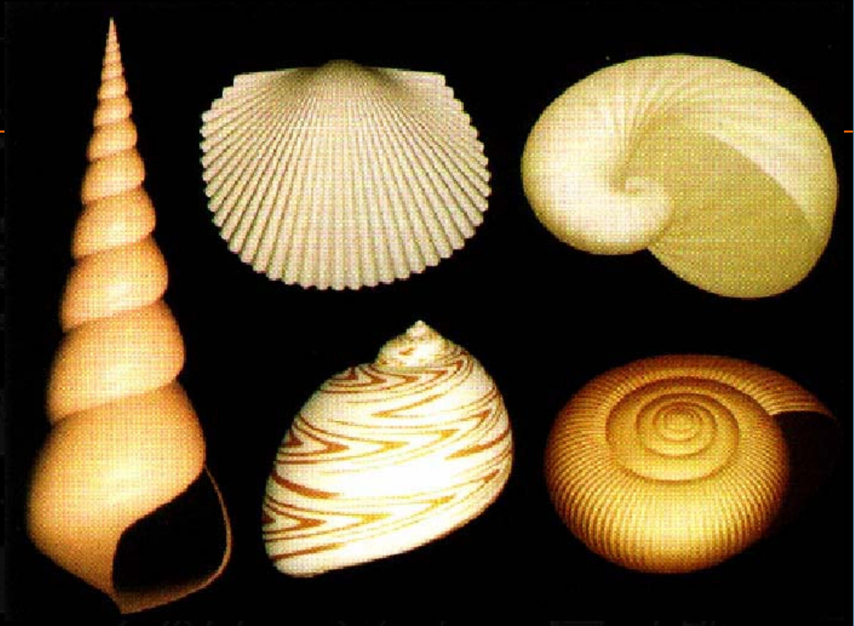
Turing Patterns in a Chemical Medium

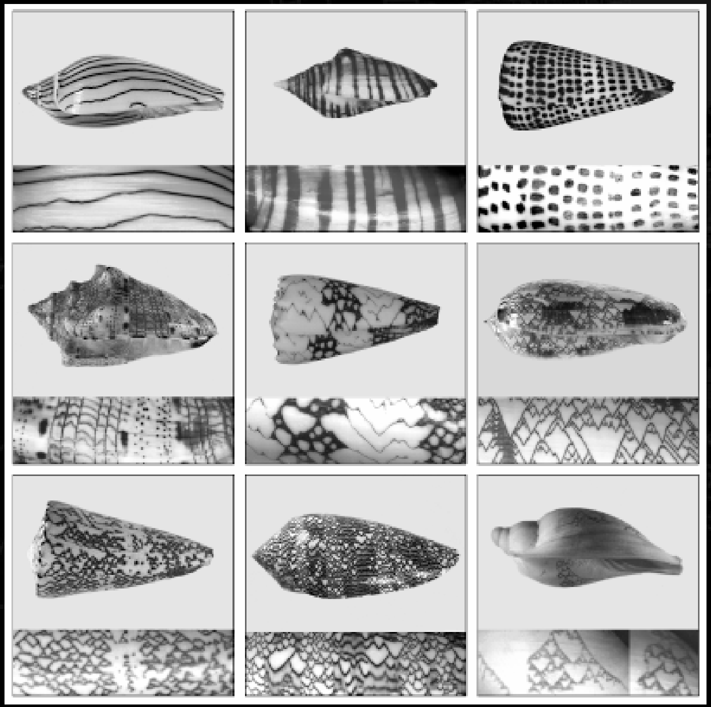
Patterns arise spontaneously through competition between localized autocatalytic chemical reaction and long-ranged diffusion of a substance inhibiting the reaction

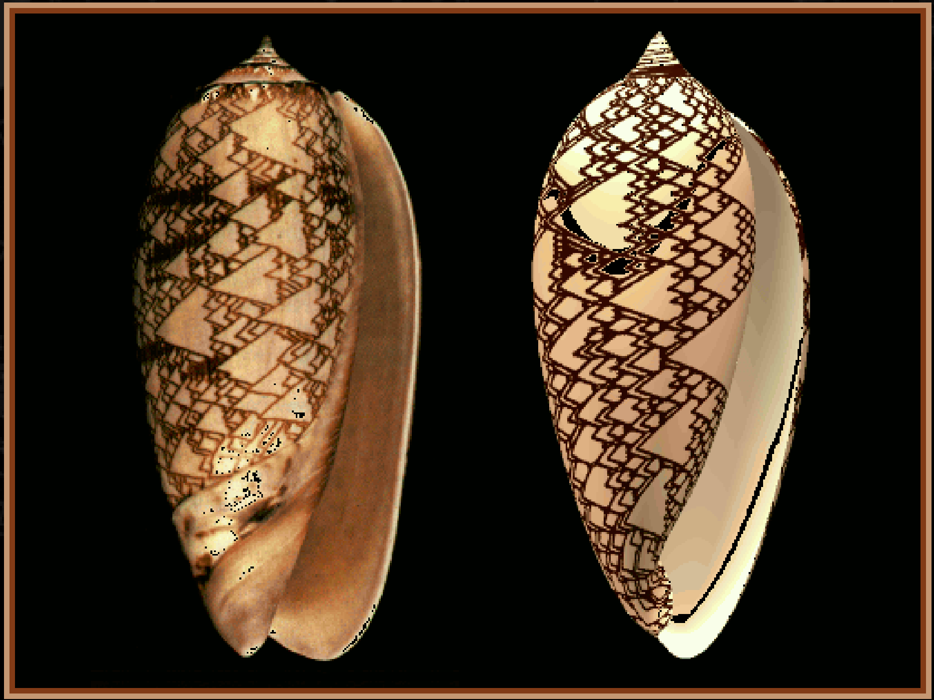


Results: Often Surprising!









Activator-Inhibitor System

- Short-range autocatalysis / long-range inhibition
- Local instability but global stabilization
- Behavior of system is often difficult to predict (fluctuations in initial conditions render accurate predictions impossible)