Chaos, Complexity, and Inference (36-462)

Lecture 11: Excitable Media

Cosma Shalizi

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Today: excitable media

1. Example of common real-world mechanism for pattern formation
2. Can be modeled by cellular automata
3. Can understand the CA in some analytical detail

Two truly excellent books to read if this is at all interesting: Winfree (1980, 1987)

Excitable Media: The Heart

Some facts about heart tissue:

Muscle cells work by contraction
Contraction needs electrical/chemical stimulation
Contraction works by pumping some chemical out of the cell and others in
Contraction is followed by “refractory period” (reversing the chemical pump)
Refractory cells cannot be excited into contraction
After refractory period cells *can* be excited but do not *spontaneously* contract
Contracting cells produce electrical pulses which stimulate neighbors
The heart is a closed manifold
Pacemaker node

Network of special fibers for conducting stimulation (“anastomosis”)

Wiener and Rosenblueth (1946)

regular contractions, spiral waves, scroll waves

Abstracting the mechanism

Three basic sorts of behavior:

Quiescent	Standing around waiting; can be excited
Excited	Doing something right now
Refractory	Recovering from having been excited, cannot be excited but does return to quiescence eventually

Assumption: excitation *spreads*, somehow, *locally*

What this leaves out:

nature of excitation; mechanism of spread

geometry of heart; change of geometry due to contraction

nature of quiescence

pacemaker; conducting fibers

"Excitable medium" is an **abstraction** and a **mechanism**

Abstraction

Selects out certain features, hides others as details

math, software engineering

Promises — if the abstraction is valid — that if you somehow implement those features, that behavior, you can count on it to obey those rules

Requires that you not rely on any of the details of *how* they are implemented, or even get to know what they are

"restricted interface", "handles" (Krieger, 1992)

Emergent macroscopic variables are abstractions

Finding good abstractions is difficult

In the social world, institutions work hard to *make* abstractions valid (Stinchcombe, 2001)

This is essentially *mathematical* thinking (Kitcher, 1983)

> *The first things I found out were that all mathematical reasoning is diagrammatic and that all necessary reasoning is mathematical reasoning, no matter how simple it may be. By diagrammatic reasoning, I mean reasoning which constructs a diagram according to a precept expressed in general terms, performs experiments upon this diagram, notes their results, assures itself that similar experiments performed upon any diagram constructed according to the same precept would have the same results, and expresses this in general terms.*
>
> *— C. S. Peirce (quoted in Haaparanta (2001))*

Mechanism

recurring, recognizable causal pattern, sometimes but not universally valid (Hedström and Swedberg, 1998; Hedström, 2005)
like a “pattern” in software engineering
See Salmon (1984); Giere (1988); Kitcher (1993); DeLanda (2006) for interesting (and useful!) philosophy on mechanisms, explanations, abstractions

Other Exciting Things

Because the mechanism is abstract, it can be applied to other assemblages

need to check that it works in each case

neural tissue, epilepsy — neurons are also excitable cells; spreading waves of excitation are Bad Things (seizures)

chemical oscillators

slime molds

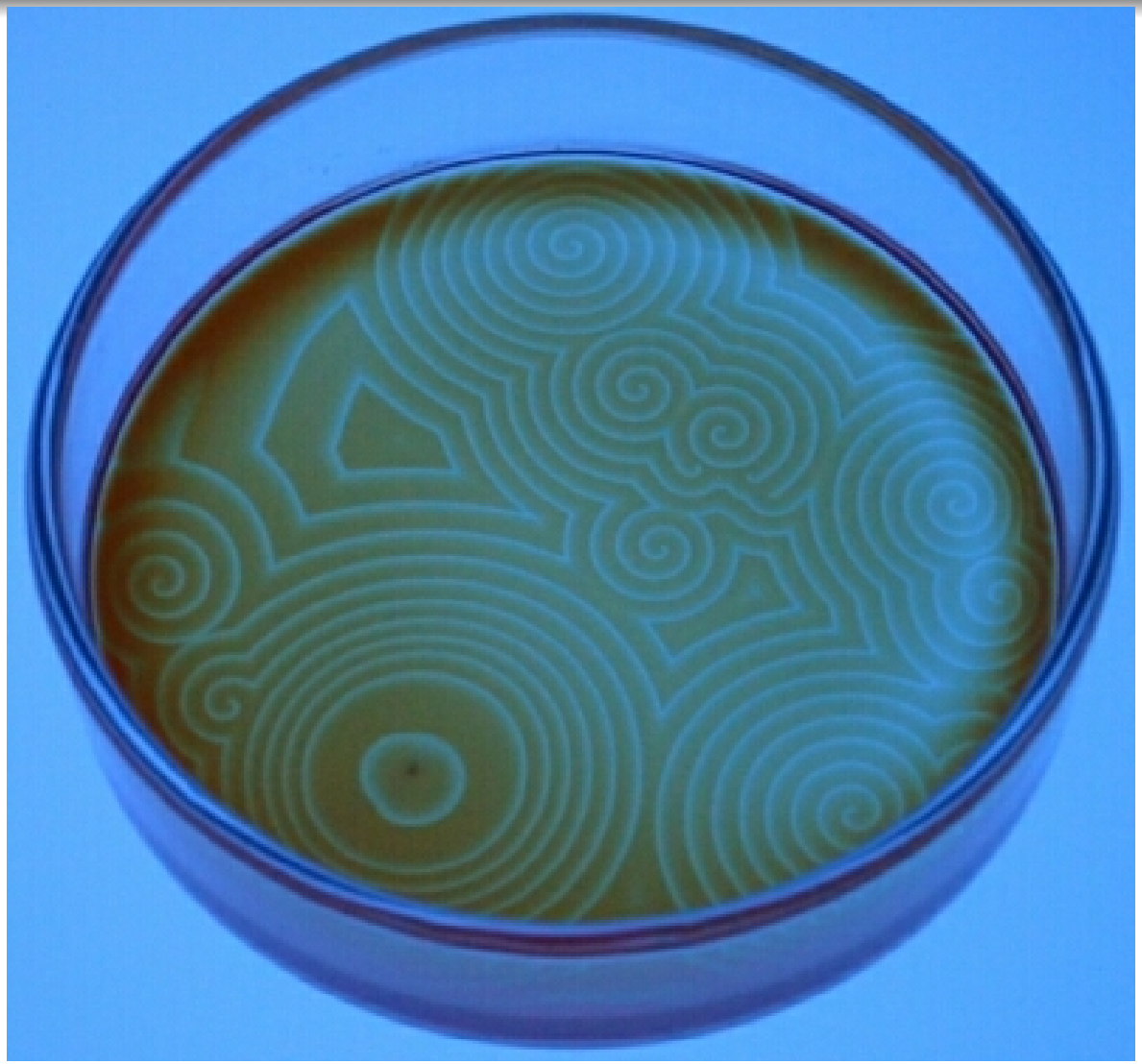
Martian ice canyons

Chemical Oscillators: Belousov-Zhabotinsky Type

A ridiculously crude caricature:

$$\begin{aligned} A &\rightarrow B \\ A + B &\rightarrow 2B \\ B + C &\rightarrow 2C \\ C &\rightarrow D \end{aligned}$$

B builds itself up from A autocatalytically
C does the same thing to A
C turns to D
ultimately reaction runs $A \rightarrow D$
autocatalytic build-up: excitation
diffusion spreads excitation
quiescence: waiting for substrate chemicals to diffuse back in



Chemical Oscillators: Turing Type

A different mechanism

$$\begin{aligned} A + B &\rightarrow 2A + I \\ I + A &\rightarrow D \end{aligned}$$

A makes more of itself and I
I makes A inert
Assume I diffuses faster than A
local activation, long-range inhibition
proposed by Turing for plants, later proposed for animals
doesn't seem to work like that
but can be realized chemically

Turing in Action: City Formation

Where to put your shop/factory/house?

after Krugman (1996); Fujita *et al.* (1999)

but see also Page (1998); Henderson *et al.* (2001)

Near others (positive feedbacks): share supplies/infrastructure/resources, customers, short travel times

Away from others (negative feedbacks): avoid competition, "nobody goes there any more, it's too crowded" (land prices)

Local activation (positive feedback), long-range inhibition (negative feedback)

Chance concentrations will grow, but also inhibit growth of close competitors

principles also apply within cities

see Rietkerk *et al.* (2004) for *ecological* cases

Tysons Corner, VA, *circa* 1962: One corner, gas station
Lots of cross-roads like this in northern VA near DC

Tysons Corner, VA, *circa* 2006
2nd largest single retail center on east coast (after NYC)

http://www.washingtonairports.com/service/Healthy%20Economy.pdf

Turing-type oscillators are *not* excitable media

high *A* concentration isn't excitation, can be self-sustaining

Both are **reaction-diffusion mechanisms**

R-D is yet more abstract than either Turing or excitability

Observed patterns can *look* very similar, but different dynamics

Dictyostelium discoideum

Cellular slime molds, especially *Dicty* (Bonner, 1967, 2009)
Life cycle:

- **Free-living** amoebae, crawl around eating bacteria, fission
- **Aggregation** response to stress
- **Slug, "grex"** Forms single mass, differentiated, responsive, crawls uphill
- **Fruiting body** Differentiates into stalk/spores, latter disperse

Mathematical modeling of aggregation goes back to Keller and Segel (1970)

See Johnson (2001) for nice account of the science and its history here, Bonner (1974, 1988) for wider implications; Marée and Hogeweg (2001) is first model (CA-based) for full cycle

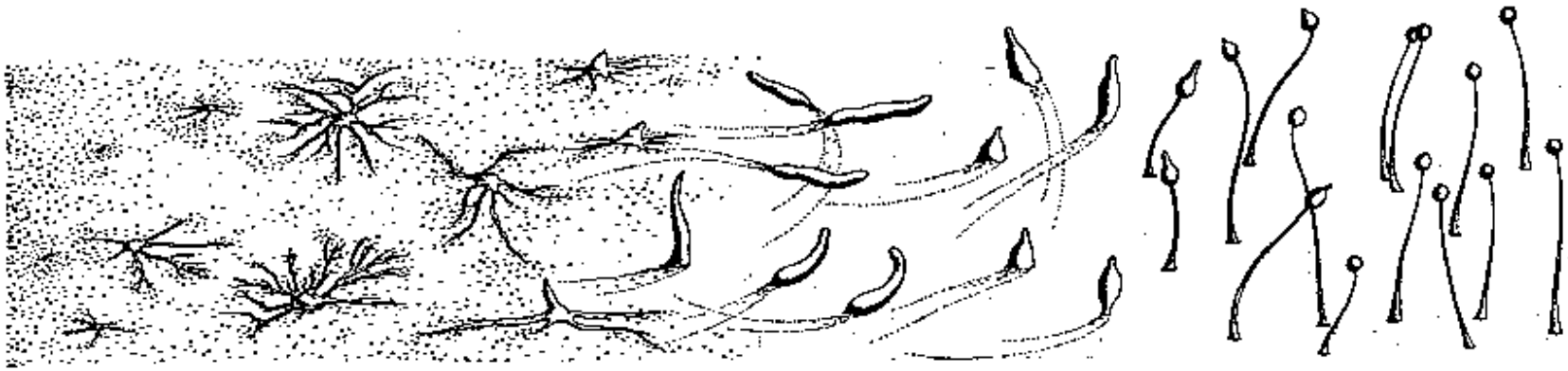
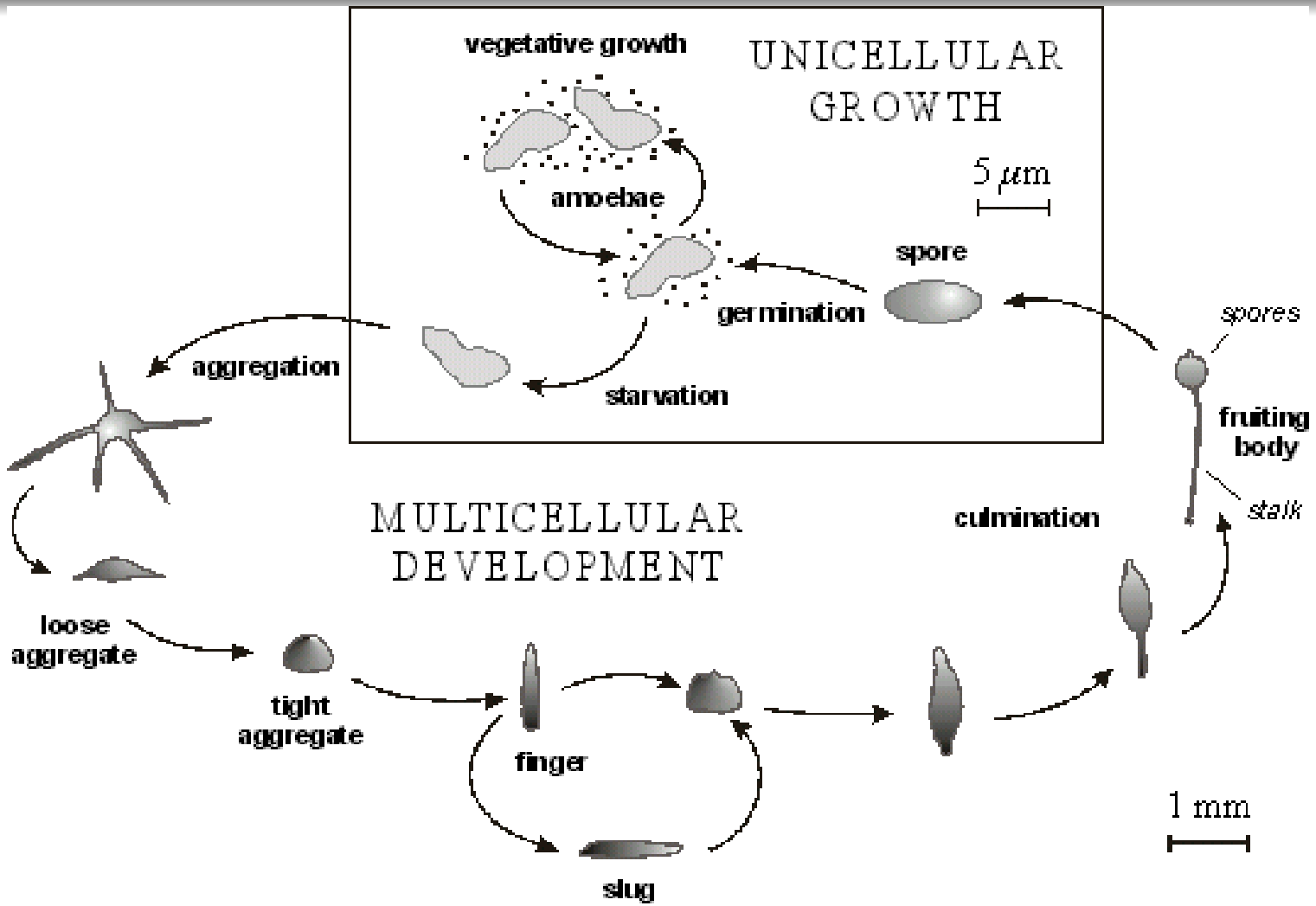
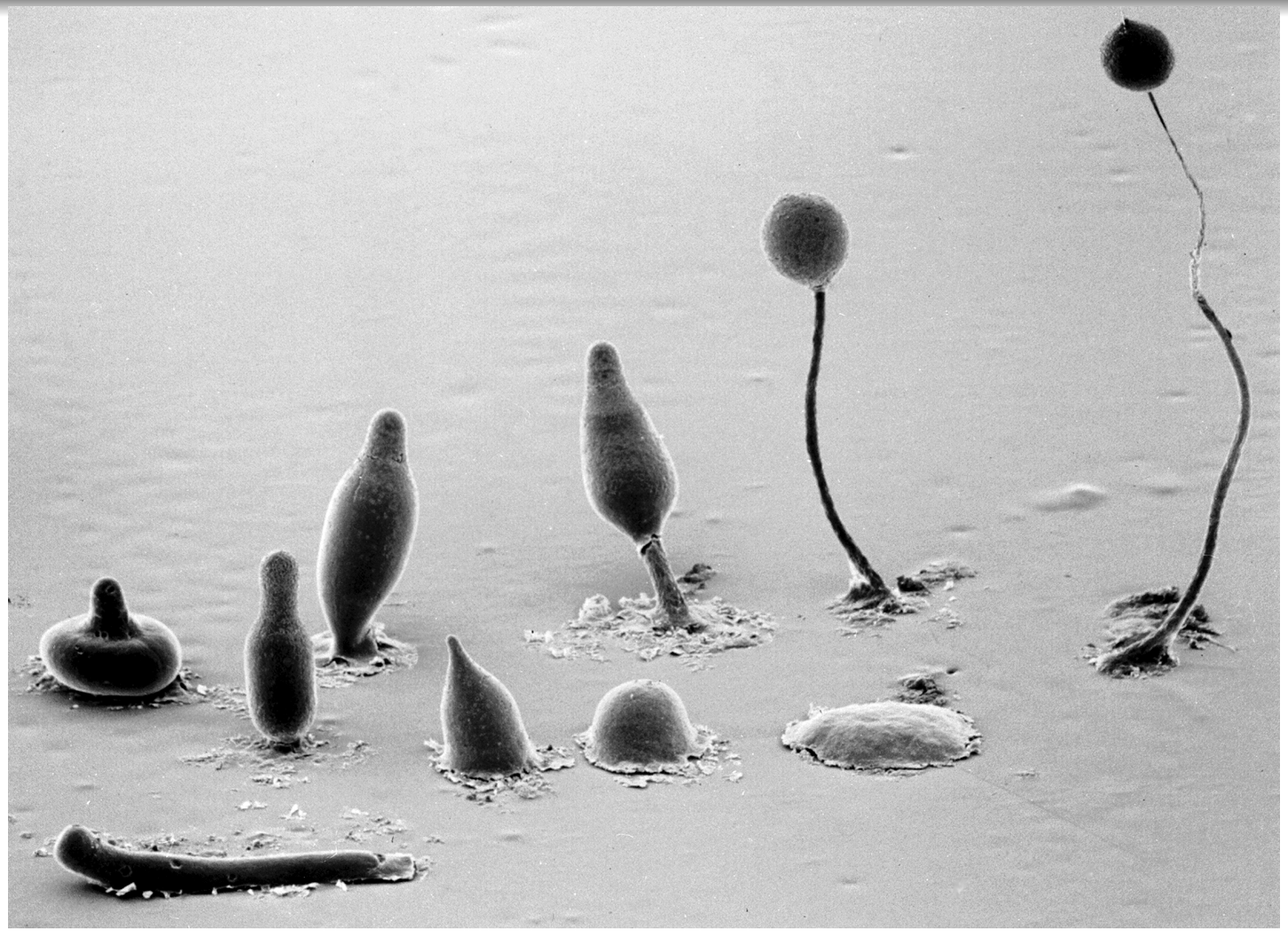


Fig. 1. The life cycle of *Dictyostelium discoideum* from the feeding stage (*left*), through aggregation, migration, and the final fruiting (*right*). (Drawing by Patricia Collins, *Scientific American* 1969)

From Bonner (2009). Note DLA-like aggregation patterns.



From Wikipedia, s.v. “Dictyostelid”



Development stages; copyright, M. J. Grimson & R.L. Blanton, Biological Sciences Electron Microscopy Laboratory, Texas Tech University; via dictybase.org

Aggregation: the amoeba

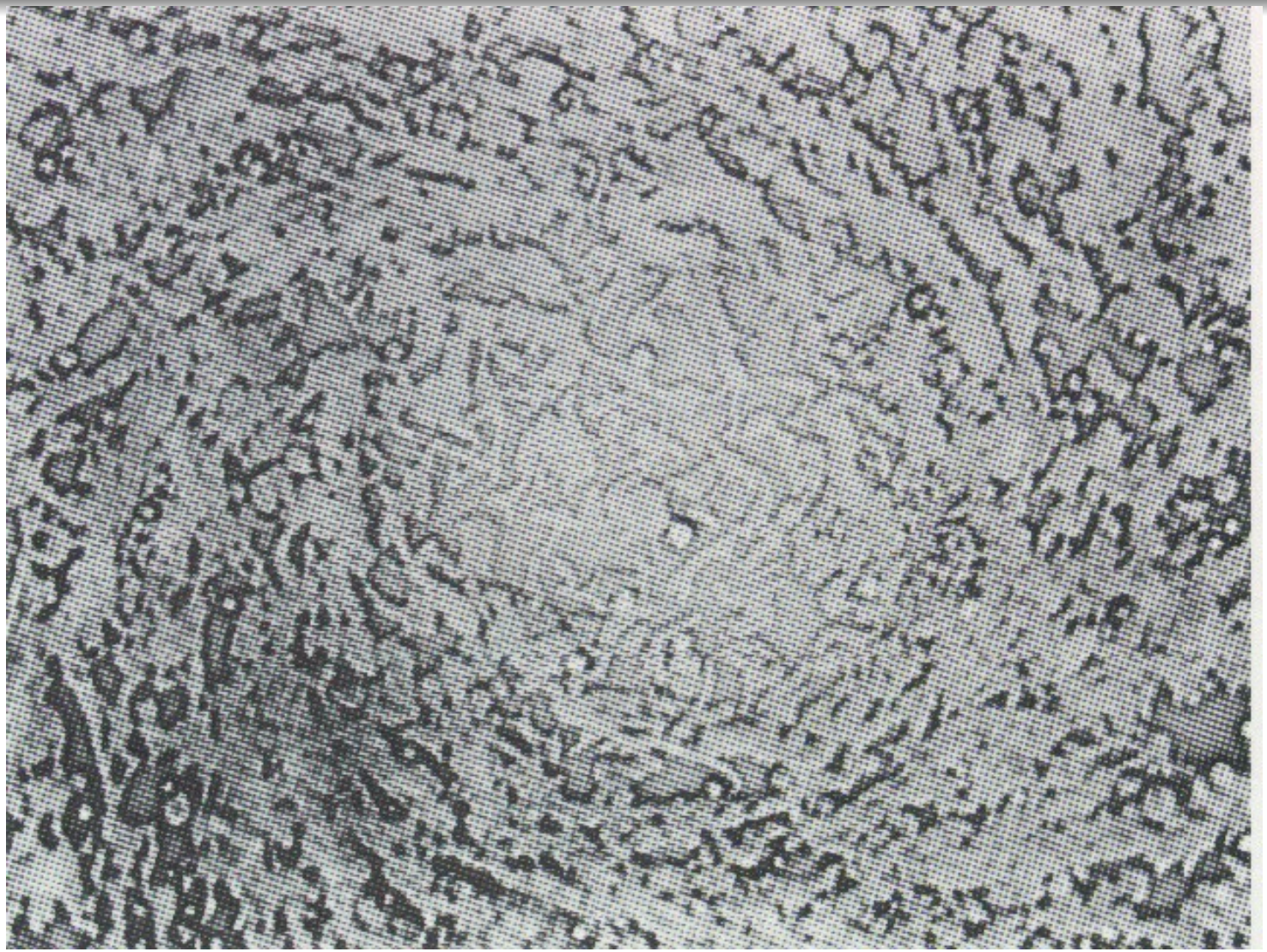
1. senses messenger chemical (cAMP) by receptor protein at cell wall (stimulation)
2. extends pseudopod in direction of chemical, crawls (excitation)
3. emits its own pulse of cAMP (spreading)
4. de-activates receptor (refractory)

messenger identified as cAMP in Konijn *et al.* (1967)

but a lot was known about the messenger *before* it was chemically identified (Bonner, 1967)

Someone has to start it; generally response to hunger

Mutations in the genes for these proteins reliably affect pattern formation (Sawai *et al.*, 2005)



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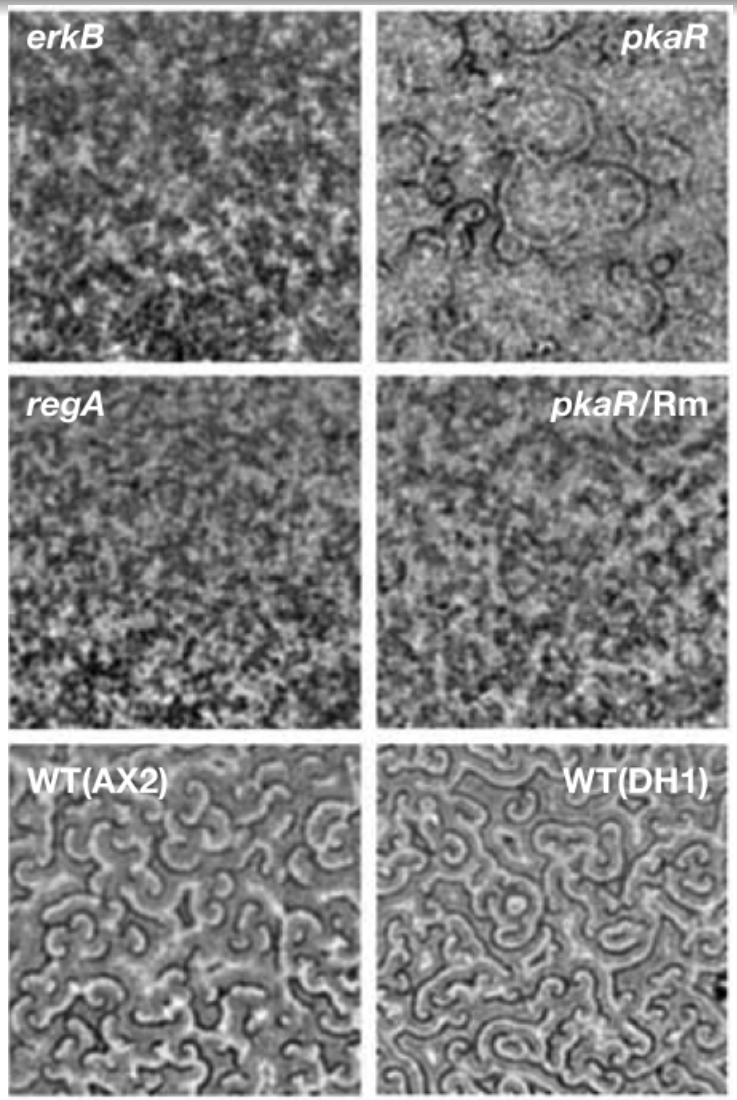
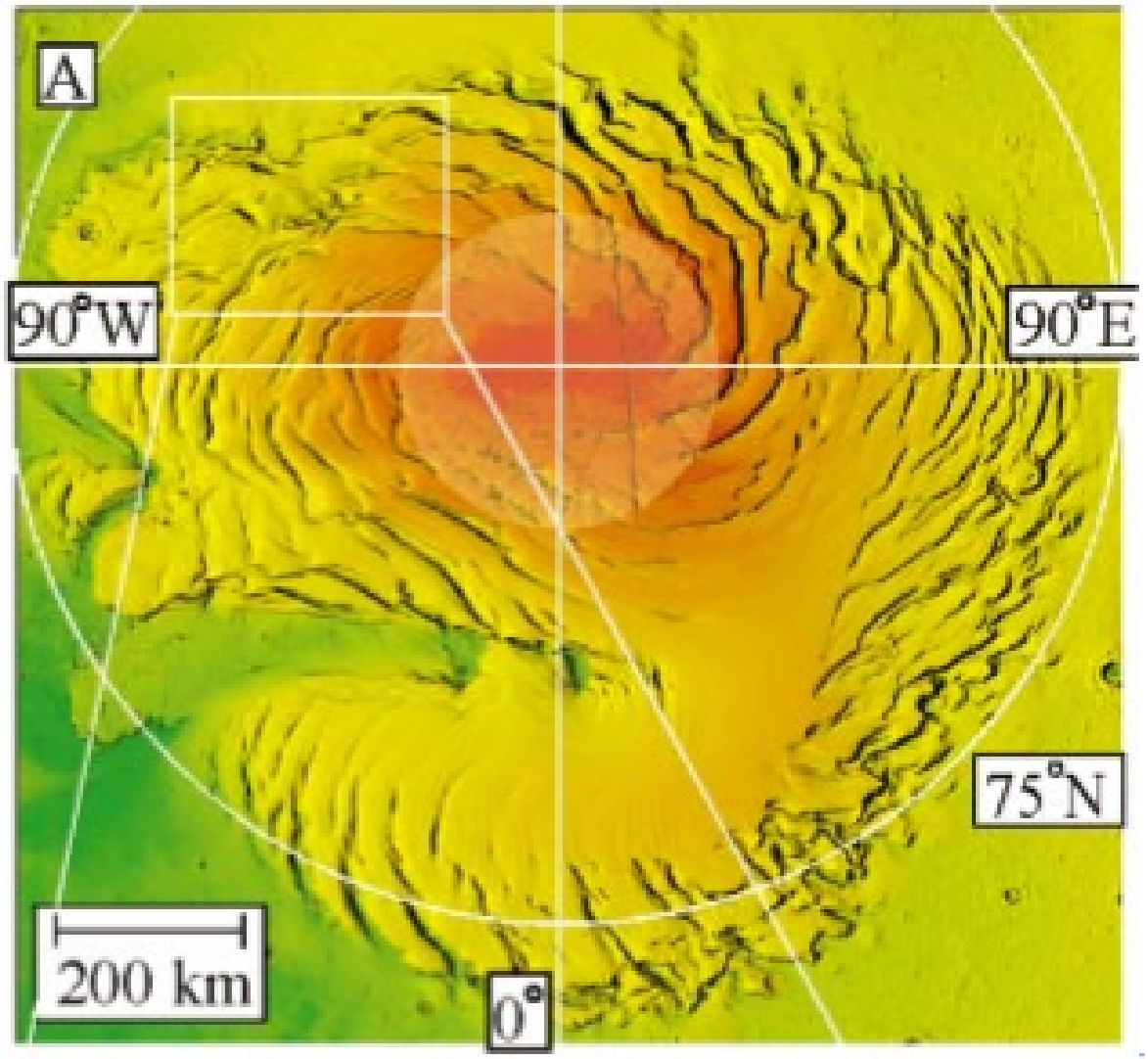
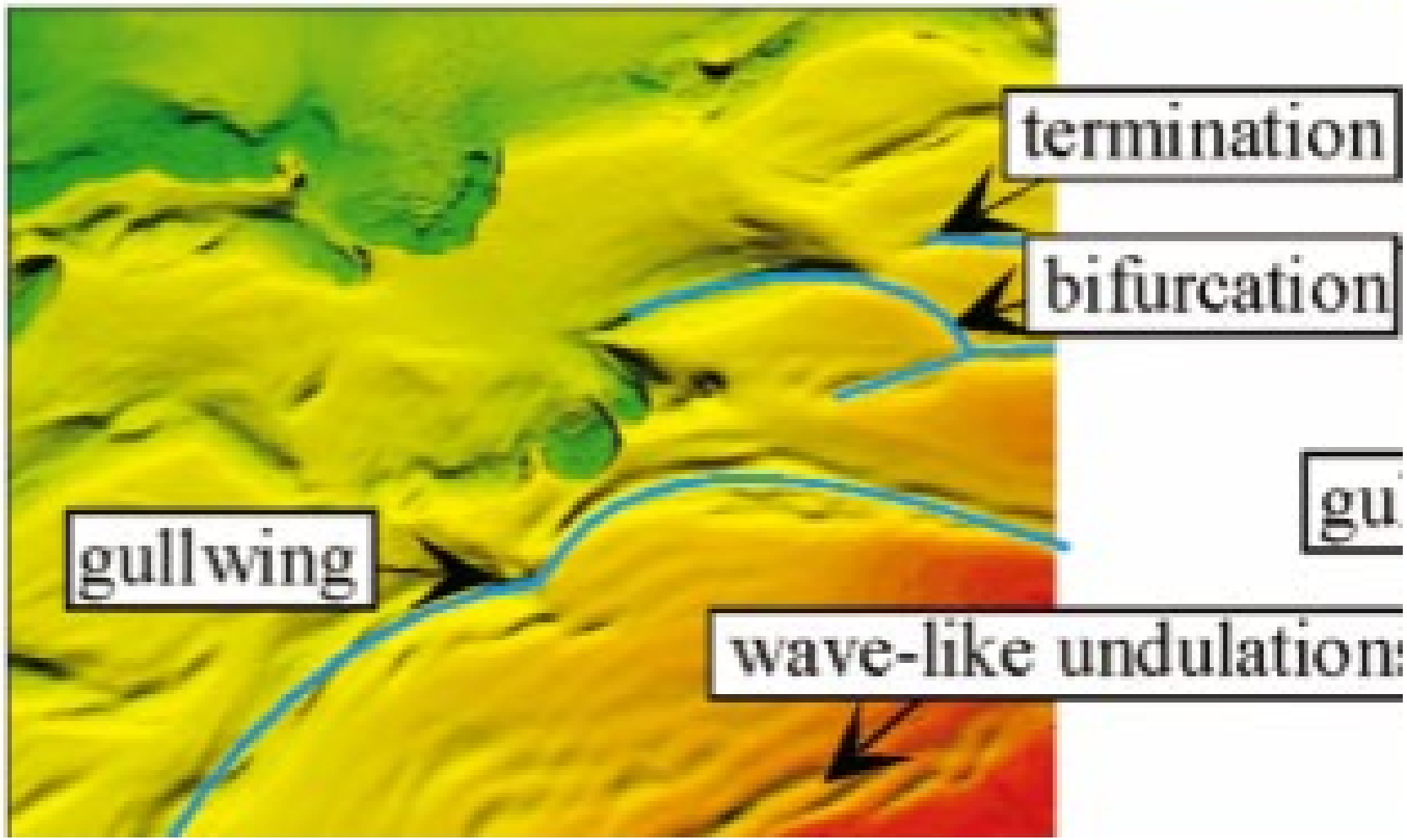


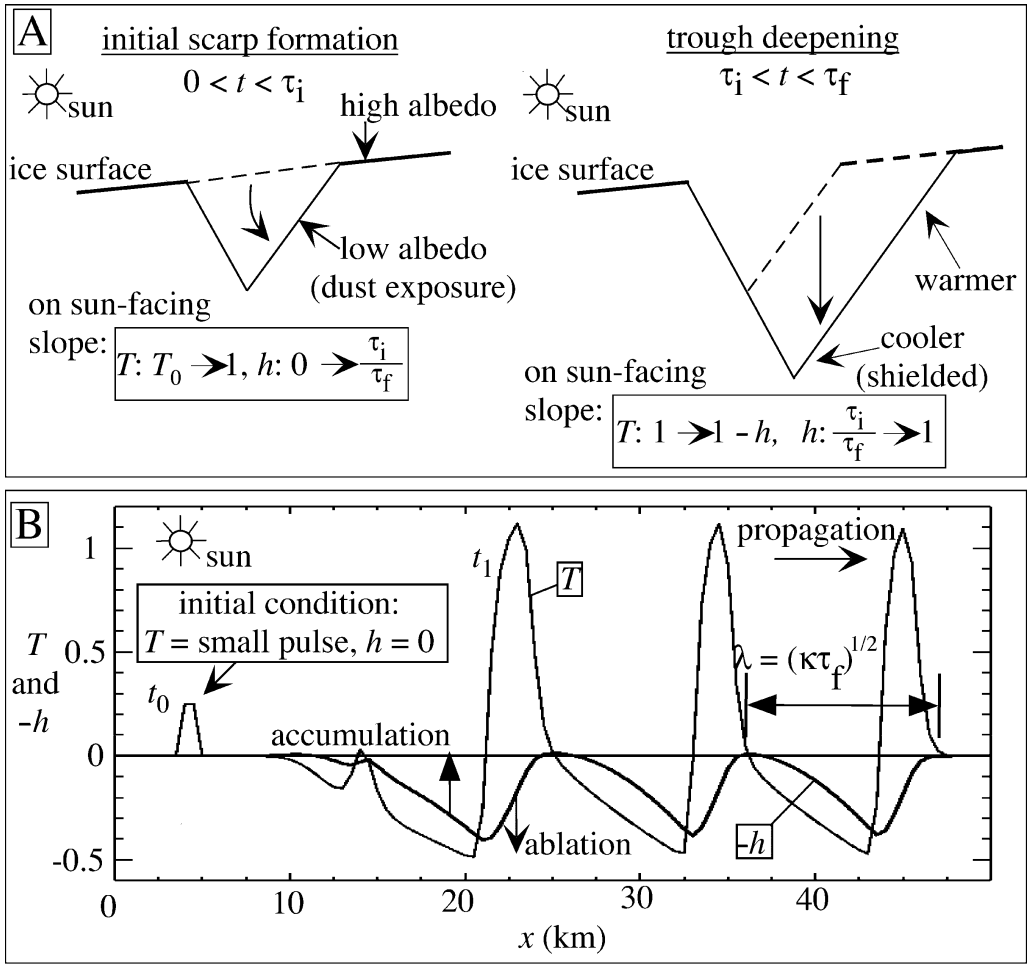
Mutants (top 2 rows), wild type (bottom row) Sawai *et al.* (2005)

Mars: Polar Ice Canyons (Pelletier, 2004)





closeup (Pelletier, 2004)



$h =$ depth, $T =$ temperature (Pelletier, 2004)

ice melts on sunny side, condenses on shady side, hole gets deeper and steeper

Greenberg-Hastings CA

Greenberg and Hastings (1978)
$\kappa \geq 3$ states, radius of rule ρ
state 0: resting/quiescent
state 1: excited
states 2 through $\kappa - 1$: refractory
$0 \rightarrow 1$ if $\geq \theta$ neighbors are 1
$k \rightarrow k + 1$ mod κ, automatically, if $1 \leq k \leq \kappa - 1$
$\kappa - 2 =$ length of refractory period

Cyclic CA

Fisch *et al.* (1991a,b)
Get rid of absolute refractory period, make model more symmetric
$\kappa \geq 3$ states, radius of rule ρ
$k \rightarrow k+1 \mod \kappa$ if $\geq \theta$ neighbors are $k+1 \mod \kappa$
each color "eats" the one before it in the cycle
think of a closed cycle of autocatalytic reactions

The Basic CCA Story

Debris	regions where nothing will change (immediately)
Droplets	region with active dynamics
Defects	points where phase is discontinuous, **organizing centers** of spirals
Demons	minimum-period spirals

Debris shrinks at the expense of droplets, droplets are organized by defects, demons extend their tentacles and cover everything

Winding Number

Suppose we have a 2D curve around the origin ℓ
winding number $w(\ell)$: how many times it goes around origin counter-clockwise (net)
in calculus:

$$\begin{aligned} w(\ell) &\equiv \int_\ell d\theta \text{ (polar)} = \frac{1}{2\pi}\int_\ell \frac{x}{x^2+y^2}dx - \frac{y}{x^2+y^2}dy \text{ (Cartesian)} \\ &= \frac{1}{2\pi i}\int_\ell \frac{dz}{z} \text{ (complex)} \end{aligned}$$

CCA: we can't draw continuous curves so add up discrete phase changes around loop
Winding number is conserved by the CCA rule (inside droplets)

The Forms of Limiting Behavior

Extinction All cells quiescent. In GH if too few excitations; not possible for CCA

Fixation Configuration at fixed point; for CCA by "bootstrap percolation"

Periodicity: incoherent little spatial order

Periodicity: spirals

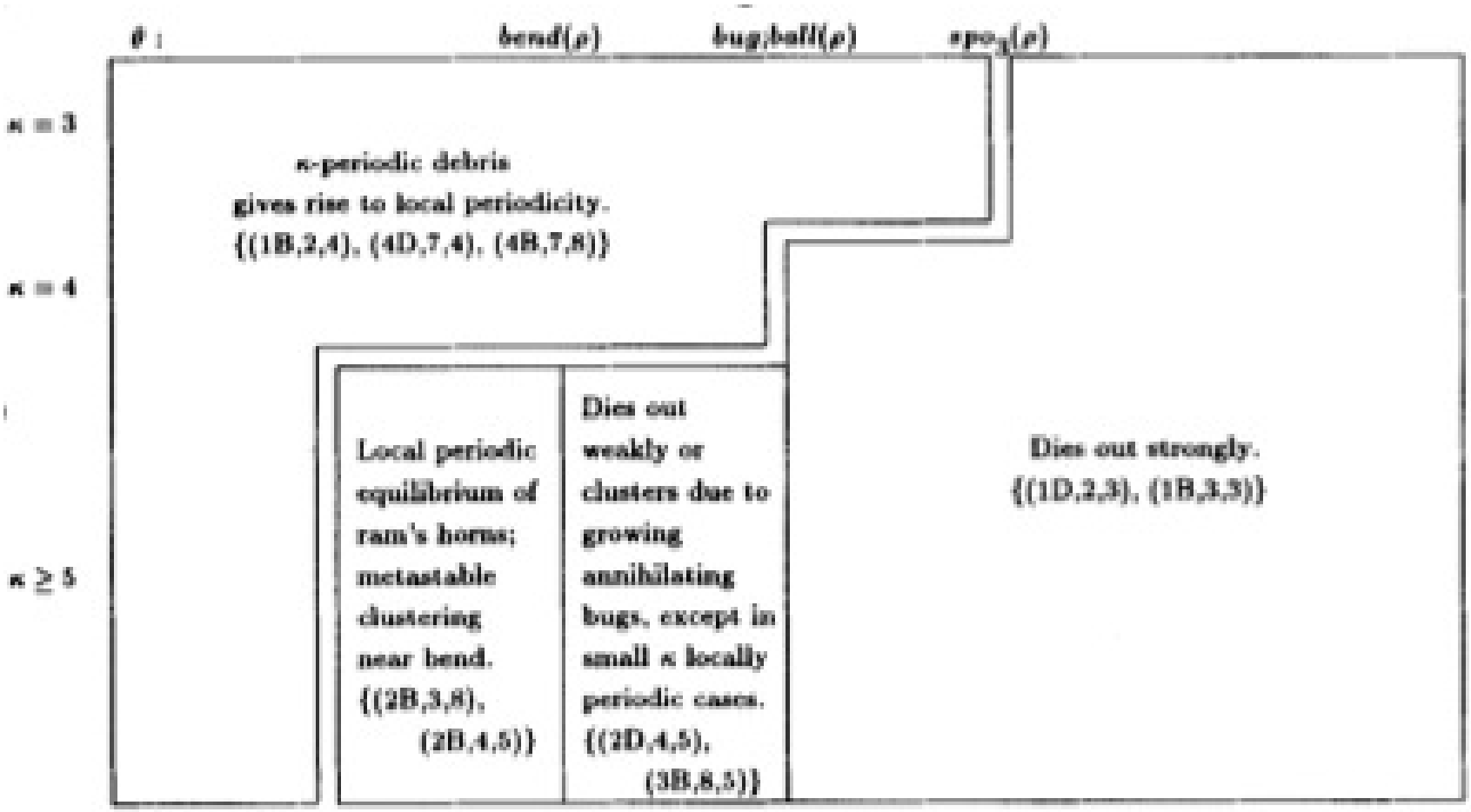
Turbulence

[simulation goes here]

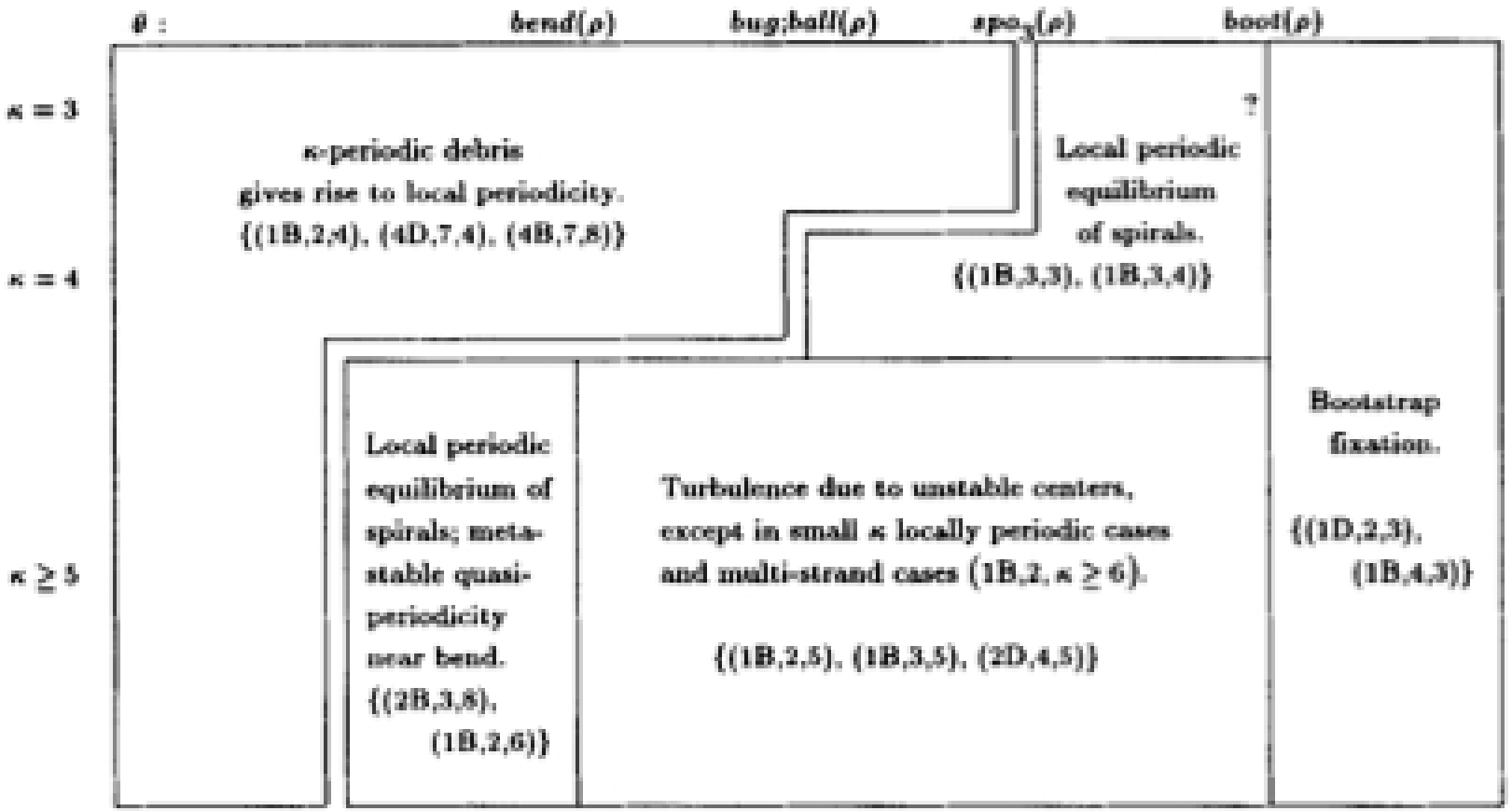
phase diagrams — qualitative behavior as a function of control settings (ρ, θ, κ)

Sharp transitions between different phases *in infinite size limit*, **metastability** at finite sizes

on following slides: phase diagrams from Fisch *et al.* (1991b)



GH phase diagram



CCA phase diagram

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