How much number theory do you have to know to be a sunflower?

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in memory of
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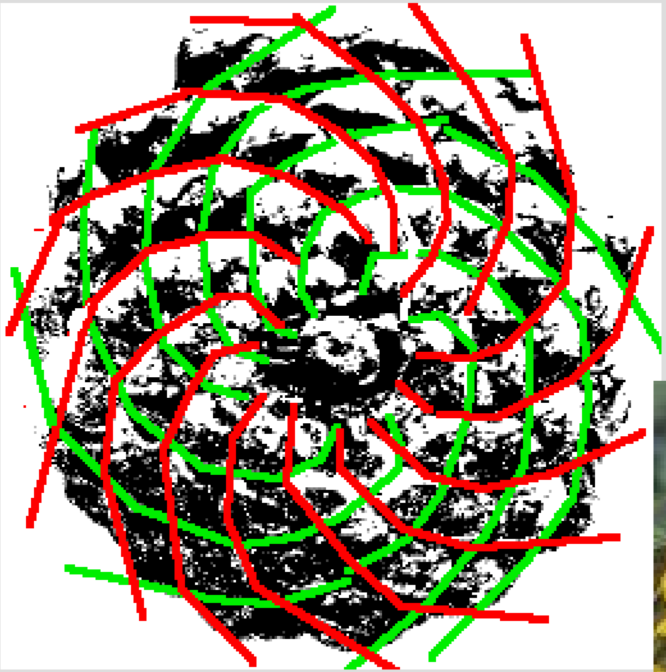
Fibonacci numbers in plant morphology

1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144...

Fibonacci phyllotaxis:
numbers of spirals (parastichies)
are consecutive Fibonacci pairs

Leaf arrangement (Goethe)



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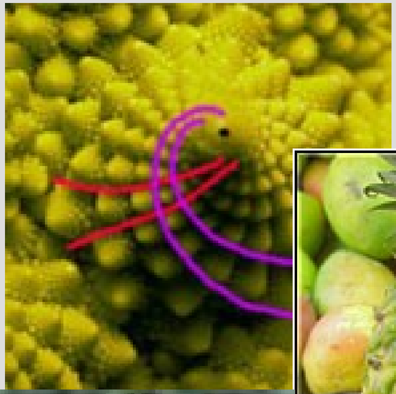
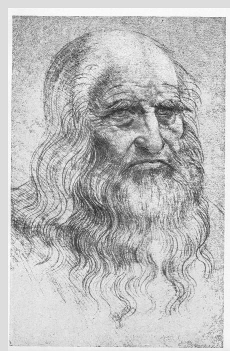


Long history: observed, characterized, systematized

Leonardo Da Vinci (Notebook 1503):

Nature has arranged the leaves of the latest branches of many plants so that the sixth is always above the first, and so it follows in succession if the rule is not impeded.



Leonardo da Vinci (1452–1519)
From a crayon portrait by himself at the Royal Library, Turin

Prof. Dr. G. van Iterson Jr.

and many, many, many others

R. V. Jean (J. Theor. Biology, 1978):

The fascinating question: "*Why does the Fibonacci sequence arise in the spirals seen in plants?*" seems to be at the heart of problems of plant morphology. In atomic physics, Balmer's series opened the way to Bohr's theory of the atom and then to quantum mechanics. The great hope of bio-mathematicians is that one day they may be able to do for biology what has been done by mathematical physicists in physics.

Non-Fibonacci numbers?

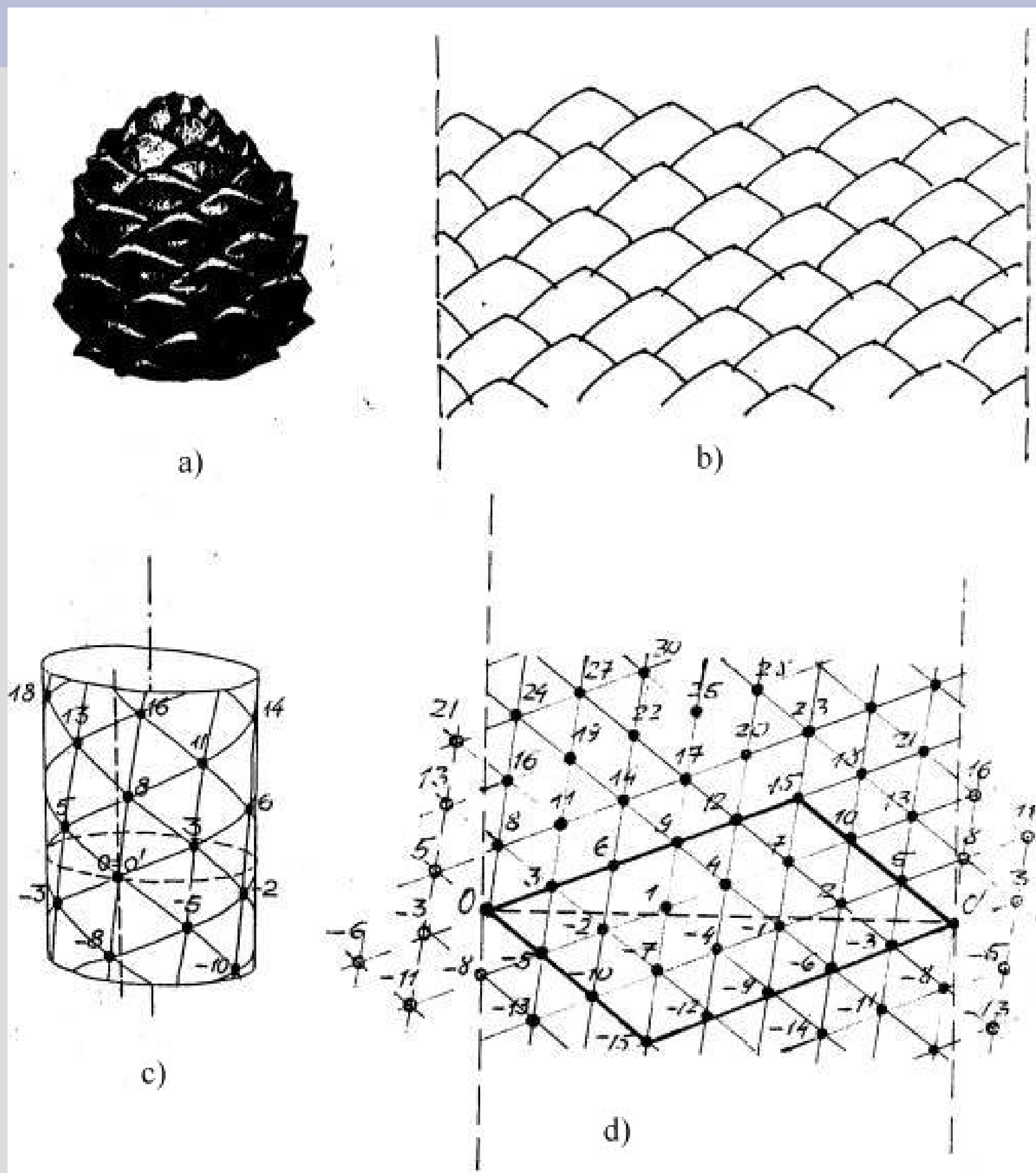
Yes, but also special:

Lucas numbers

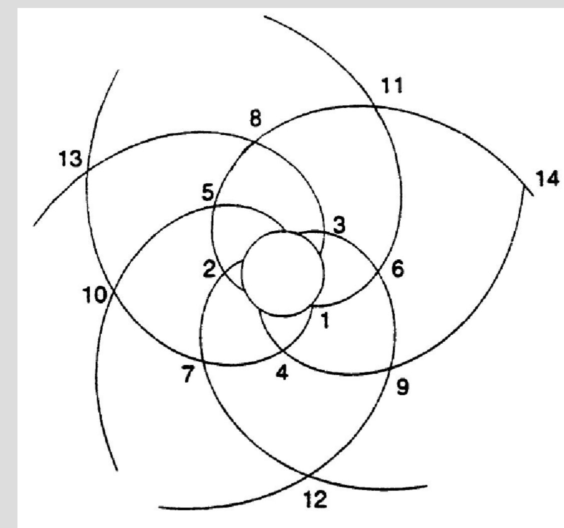
1, 3, 4, 7, 11, 18, 29, 47, 76...

Statistics for cones of pine-trees (Norway):
95% Fibonacci
4% Lucas
1% deficient

Models of phyllotaxis



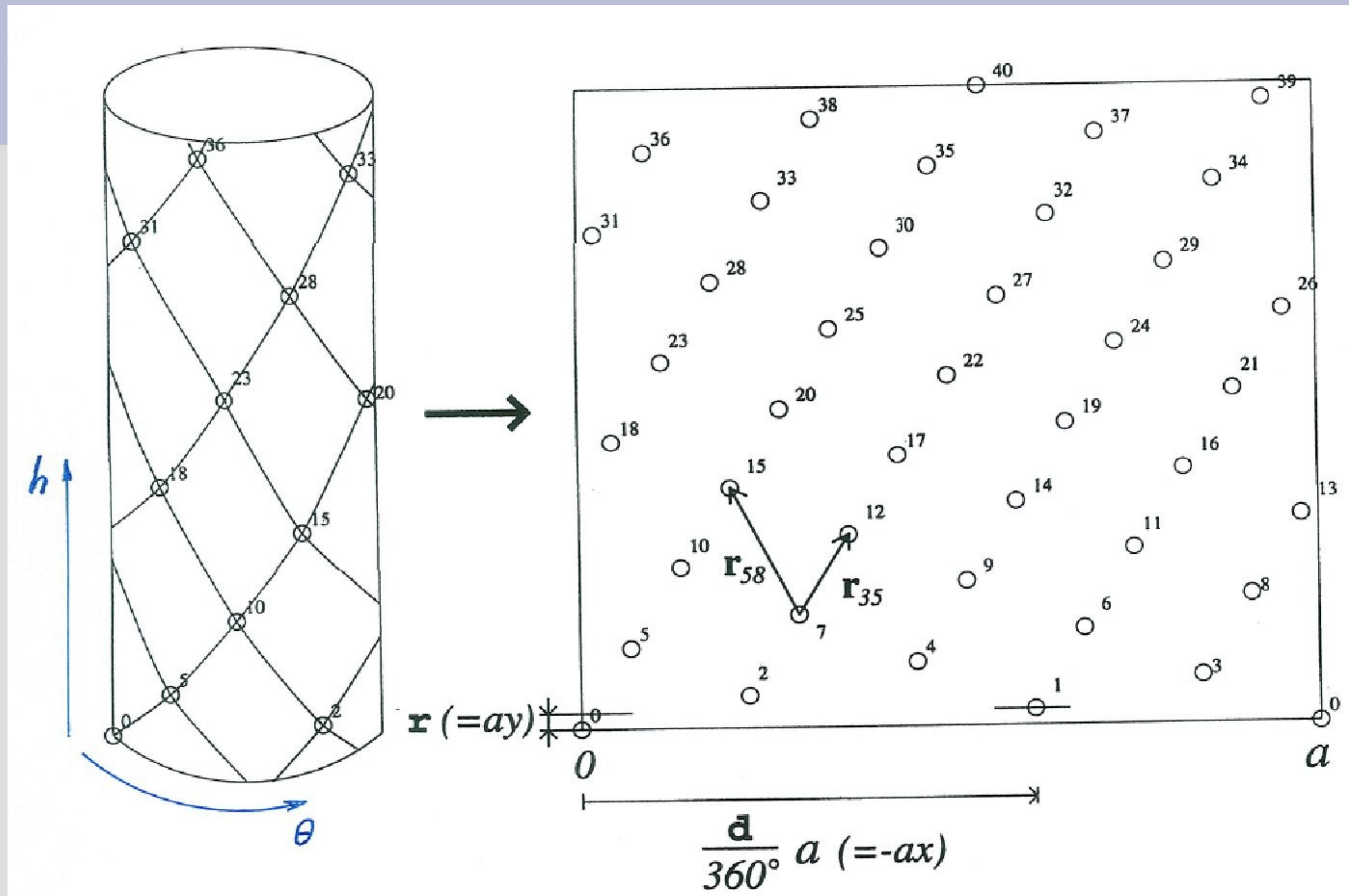
Cylindrical lattices (cones, pineapples, seed heads, etc)



(b)

Spiral lattices (not today)

Geometry of cylindrical lattices



Generating helix $h_m = \mathsf{r}\, m, \quad \theta_m = \mathsf{d}\, m$

Parastichies: lattice rows defined by **shortest vectors**

Parastichy type of a lattice: (N, M)
right left

Lattice phase space (x,y)

A more convenient parameterization: $\mathbf{r} = u\mathbf{i} + v\mathbf{j}$ (Cartesian system)

$$\mathbf{r}_{pm} = u_{pm}\mathbf{i} + v_{pm}\mathbf{j} = a\left((p - mx)\mathbf{i} + my\mathbf{j}\right) = \sqrt{A}\left(\frac{p - mx}{\sqrt{y}}\mathbf{i} + m\sqrt{y}\mathbf{j}\right)$$

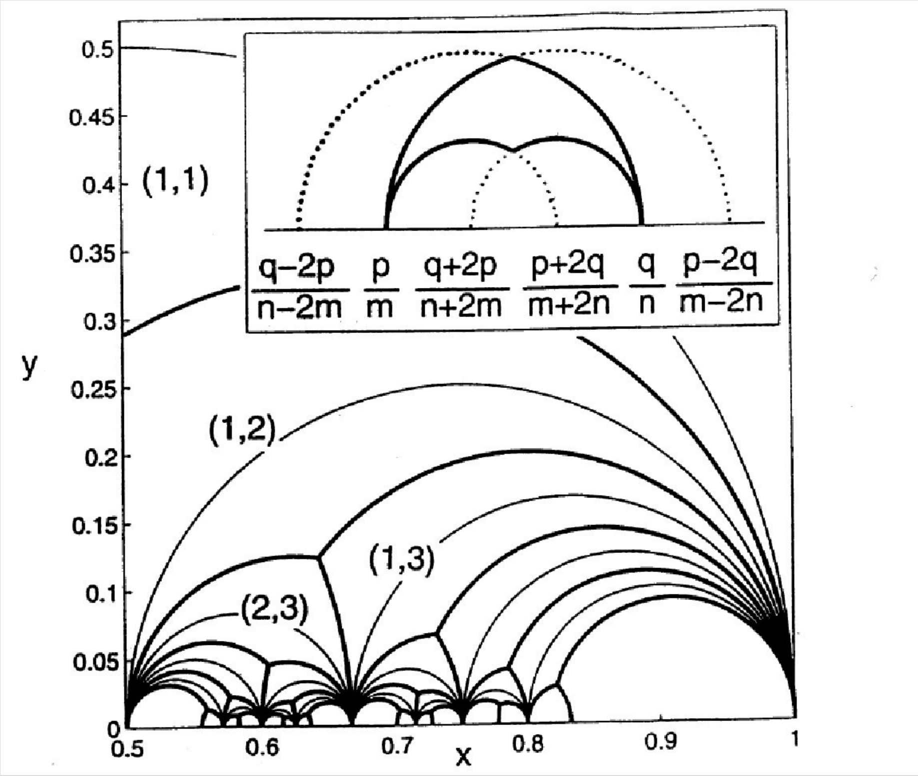
Unit cell area (A=1)

Given x and y, what are the parastichy numbers N and M?

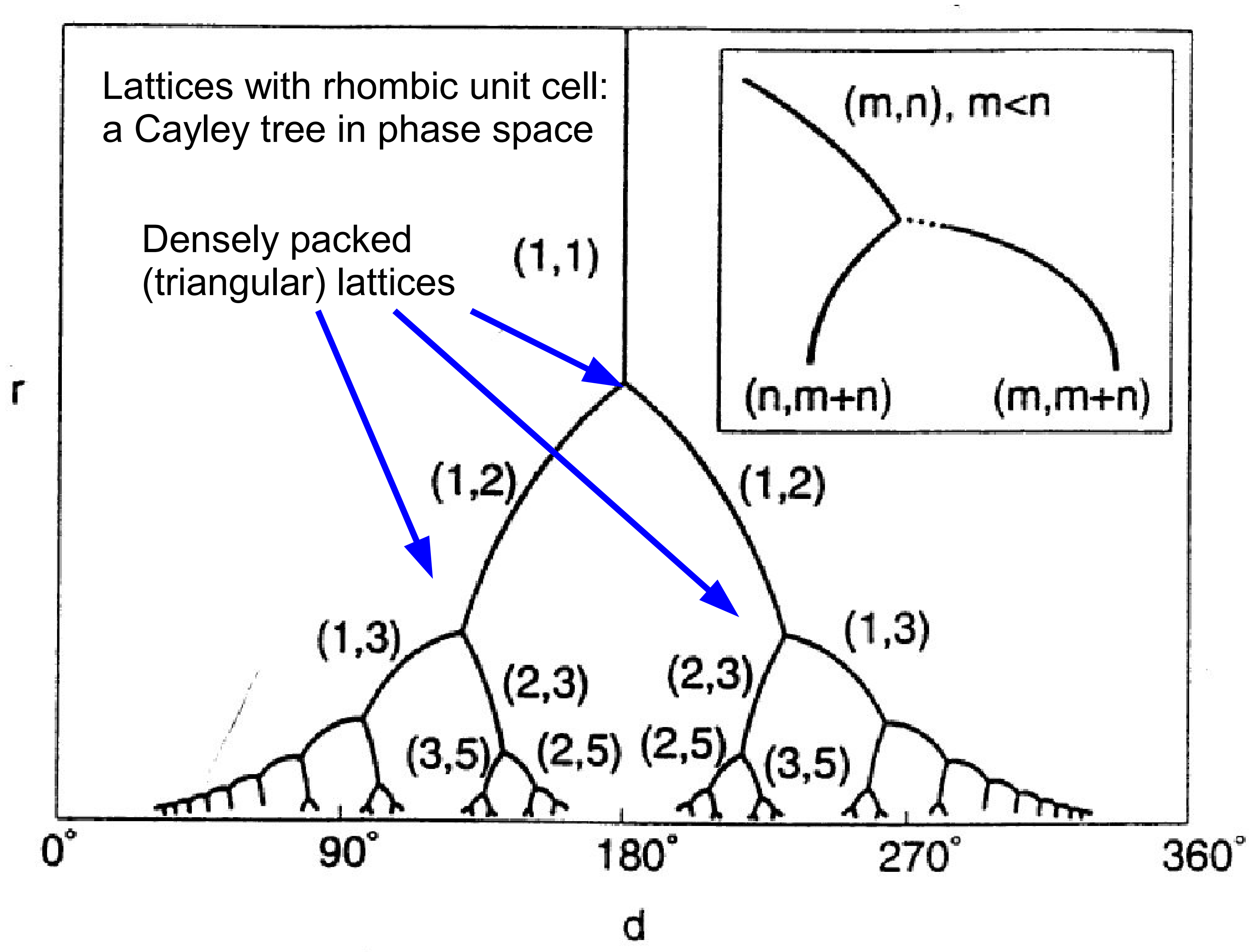
Parastichy domains in the x, y plane: domains of constant N, M

Boundaries are arcs of circles (*lattices with rectangular unit cell*) N=n, M=m;

All mutually prime N, M theoretically possible!



An interesting example: close-packed disks on a cylinder



What have we learned so far?

- Cylindrical lattices are a useful model (phase space, parastichy numbers, etc)
- Hints at connection with hyperbolic geometry: Cayley tree
- Do not explain the predominant occurrence of Fibonacci numbers (all N,M possible)

Mechanical theory of phyllotaxis

Energy model: growth under stress, phyllotactic patterns result from the development of deformation

$$E_{\text{total}} = \frac{1}{2} \sum_{pmp'm'} U(|\mathbf{r}_{pm} - \mathbf{r}_{p'm'}|).$$

The repulsive interaction U(r) models contact pressure between neighboring structural units (scales, seeds, etc) during growth

For example: $U(r) = U_0 e^{-r/r_0}$, or $U(r) = U_0/|r|^\gamma$, or $U(r) = U_0 e^{-r^2/r_0^2}$

Claim: anisotropic growth (slow axial, fast radial) deterministically generates Fibanacci phyllotactic patterns

Trajectories in the phase space

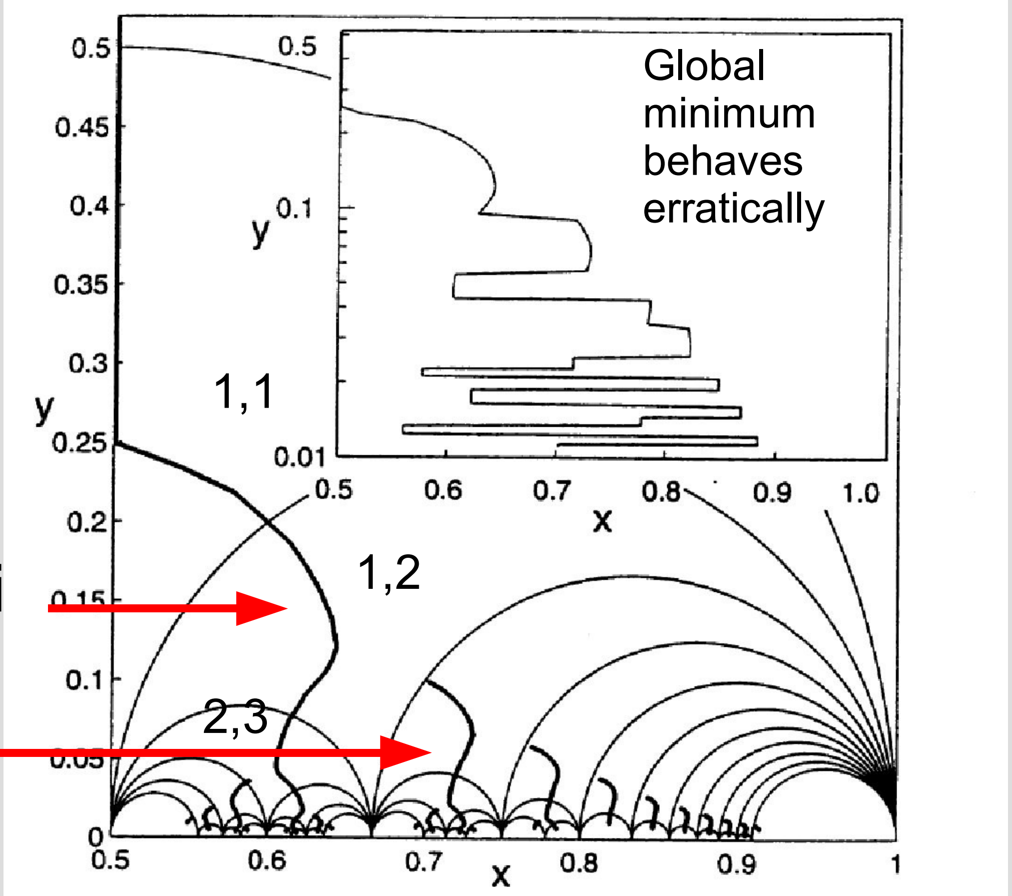
History of growth-induced deformation

$$E(x,y) = \sum_{pm} U(r_{pm}), \qquad r_{pm} = |\mathbf{r}_{pm}| \qquad A = 1$$

Track positions of local energy minima:

$$\frac{\partial E}{\partial x} = 0, \qquad \frac{\partial^2 E}{\partial x^2} > 0, \qquad A,\ y = \text{const}$$

Numerical observation: principal trajectory goes through Fibonacci parastichy domains, second principle trajectory yields Lucas numbers!



Fibonacci phyllotaxis obtained from deterministic process!

We conclude that

- By varying y and tracking energy minima all Fibonacci patterns are obtained one by one in a deterministic manner;
- Other trajectories give generalized Fibonacci sequences (e.g. Lucas);
- This behavior is robust, results do not depend on the choice of potential U(r), provided it is repulsive.

Think hyperbolic (model has analytic solution)

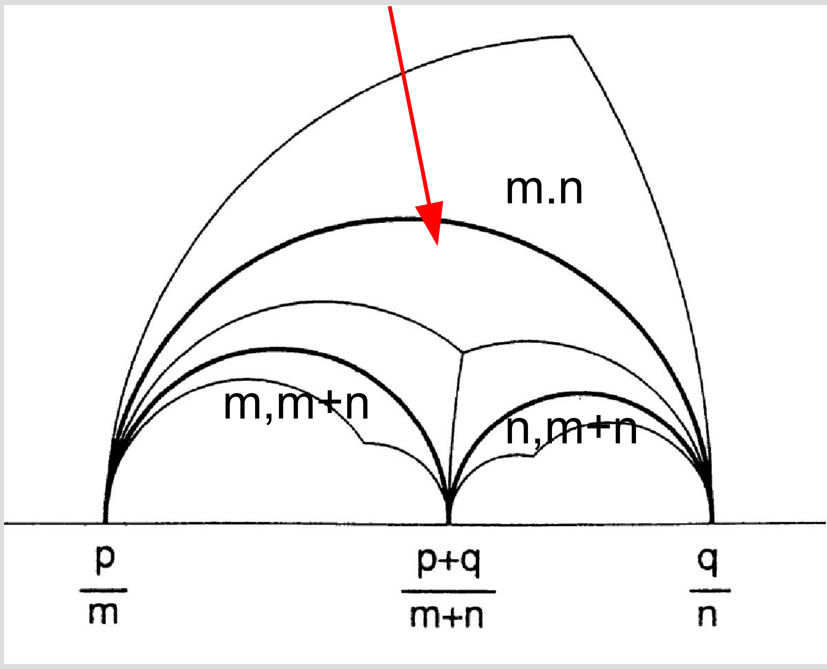
Interpret the x,y plane as a hyperbolic plane

Define curvilinear triangles with vertices
p/m, q/n, (p+q)/(m+n)   (|pm-nq|=1)

These Farey triangles partition the x,y plane
into fundamental domains of GL(2,Z)

THEOREM: The trajectories of the energy minima behave the same way in all triangles for repulsive U(r)

Proof relies on GL(2,Z) symmetry of E(x,y):
Use z=x+iy to define modular transformation
$$z'=(az+b)/(cz+d)$$
with integer a,b,c,d such that |ad-bc|=1,
then E(x',y')=E(x,y), where z'=x'+iy'.



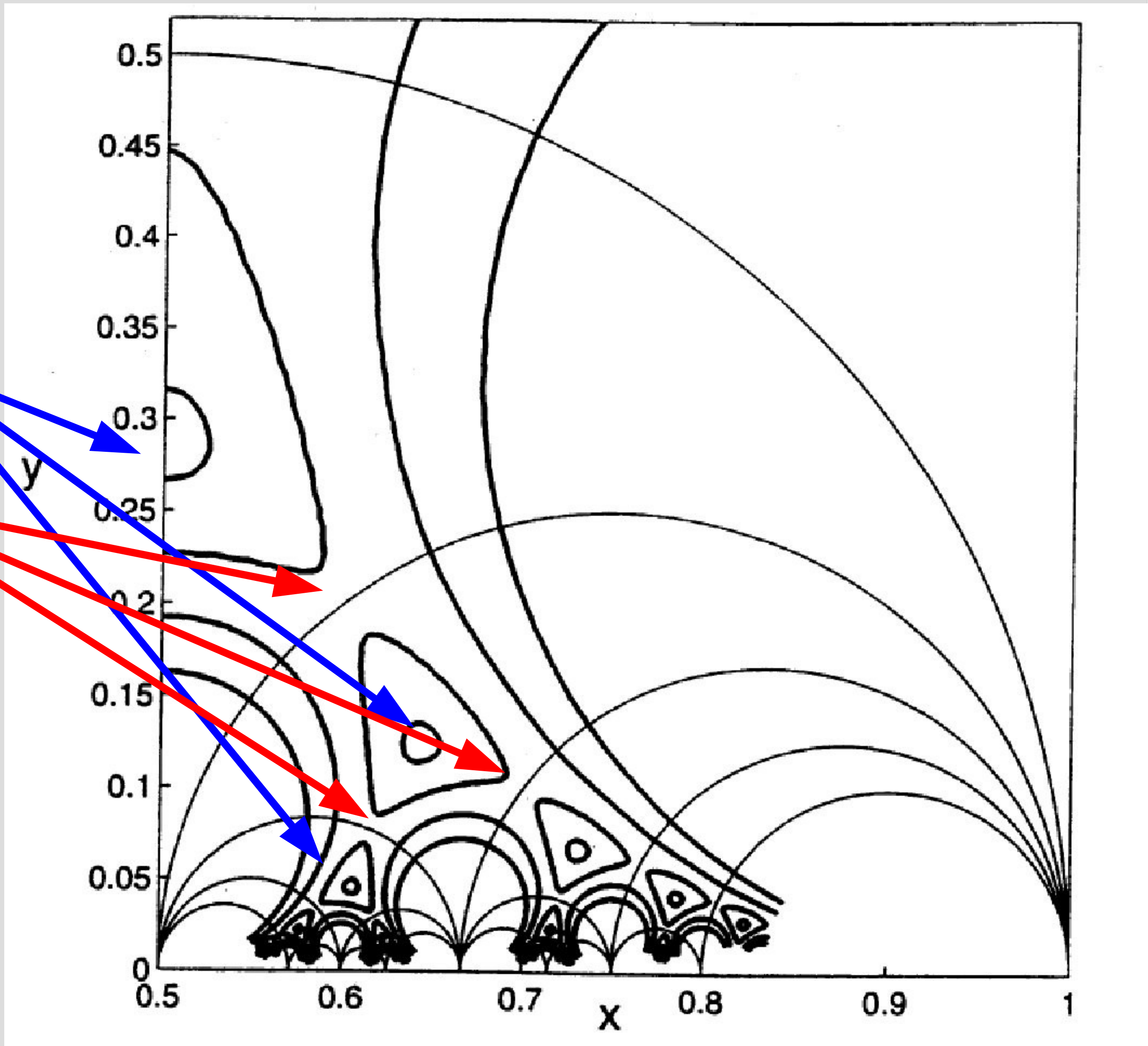
Energy E(z) landscape in the hyperbolic plane

E(z) is invariant of the modular group

Minima of E(z): perfect triangular lattices

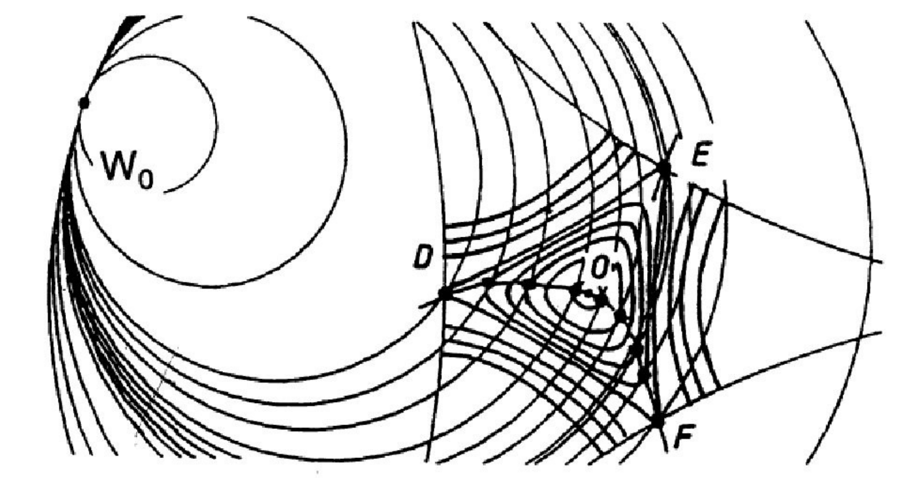
Saddle points of E(z): square lattices

Each triangle is a valley of E(z) surrounded by three ridges with three passes



Trajectories in one fundamental domain

Since E(z) is GL(2,Z)-invariant, it is sufficient to analyze behavior in just one fundamental domain



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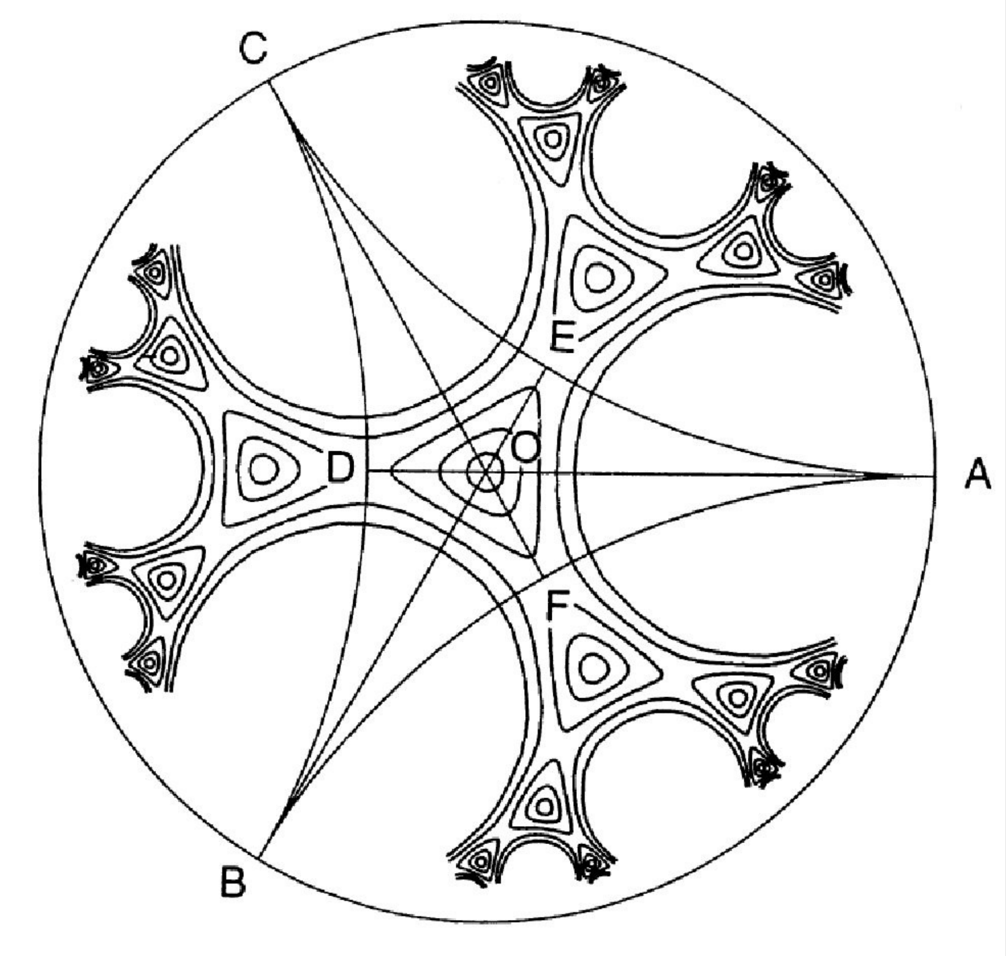
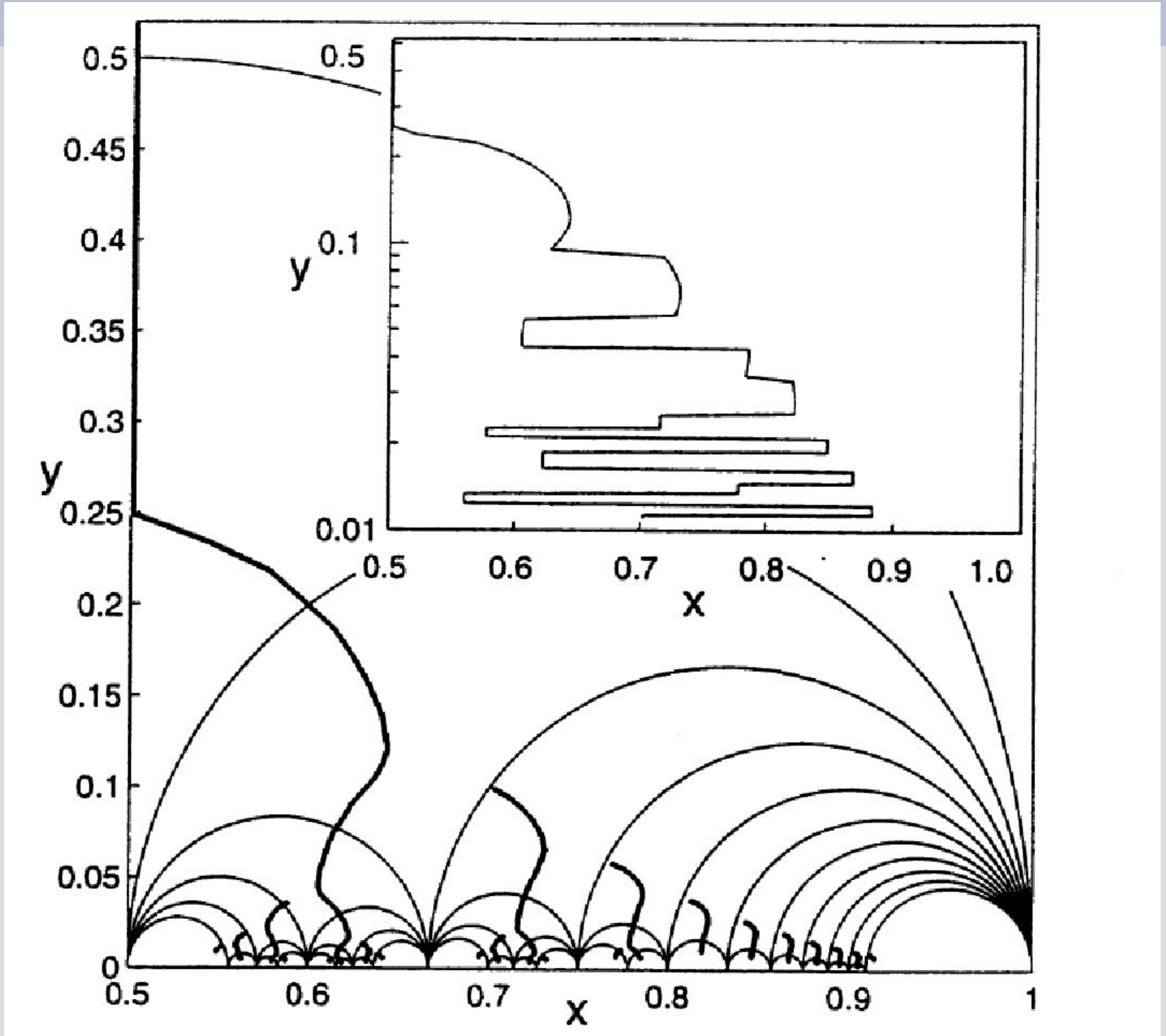


(a)

Connect trajectories in all triangles:



Summary

- **Determinism:** No bifurcations (except one where left/right symmetry is lost). The gaps between different trajectories do not vanish;
- Principal trajectory: Fibonacci sequence
- All other trajectories are described by generalized Fibonacci sequences;
- One mistake (loss of continuity) gives Lucas sequence, the most common exception;
- **This behavior is robust:** Fibonacci phyllotaxis explained