Fibonacci numbers in botany and physics: Phyllotaxis

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Regular lattices of repulsive objects on a cylinder are analyzed. An anisotropic deformation of these lattices is considered. It turns out that this process generates Fibonacci lattices, exclusively and in a deterministic way. This result may explain the widespread occurrence of Fibonacci numbers in living organisms, if it is assumed that a deformation arises during the growth of an embryo.

The leaves, scales, petals, and seeds of many types of plants are ordered in lattices (pine cones, sunflower seeds, and pineapples are best examples). The rows of nearest neighbors in these lattices form two families of spirals, with left-hand and right-hand threads. One observes a numerical regularity called *phyllotaxis*: The number of spirals in the two families is given by the Fibonacci numbers 1,2,3,5,8,13,21,34,... . For the left-hand and right-hand spirals, one finds Fibonacci numbers which are adjacent in the sequence: (5,8), (8,13), (13,21), etc. This phenomenon, which was known to Kepler, has caused much astonishment. It has been discussed and studied by many people, among them Leonardo da Vinci, the Bravais brothers, W. Thomson, Tate, Thuring, and H. Weyl. The word "phyllotaxis" itself was proposed by the poet Goethe, who, as a naturalist, took interest in this regularity. There is an extensive popular literature on the subject.[1]

The early studies of phyllotaxis consisted for the most part of a geometric analysis of lattices on a cylinder and on a cone, and of lattices formed on a plane by logarithmic spirals.[2] At the beginning of this century, interest turned to the cause and mechanism of phyllotaxis. The most interesting results were found for a model of touching disks (Ref. 3; see also Ref. 4).

Let us consider an arbitrary lattice on the surface of a cylinder. We order the nodes of the lattice in increasing height z. We find

$$z_n = hn, \qquad \theta_n = \alpha n \quad (\mathrm{mod} 2\pi), \tag{1}$$

where h and α are parameters, and $n \in Z$ (we are assuming that the lattice does not have rotational symmetry, i.e., that all the nodes are at different heights). We now require that the nodes of this lattice be the centers of identical circles which touch each other in pairs. In other words, we imagine lattices in which the two shortest vectors are of identical length. The meaning of this model is that the seeds, scales, etc., are replaced by identical hard disks which touch each other. All such lattices, i.e., the pairs (α,h) which are distinguished by the touching condition that we have imposed, can be described without difficulty. We find a set on the α–h plane which has the structure of a Cayley tree with a coordination number 3 (Fig. 1). The branches of the tree are circular arcs. The branch points correspond to regular triangular lattices (each disk touches six neighbors), and the interior points of branches are rhombic lattices in which disks touch each other in fours. The branches of the tree are marked in pairs, and the tips are marked by sets of three integers, which give the numbers of spirals generated by the shortest vectors (three such vectors in the case of a regular triangular lattice; two in the case of an orthorhombic lattice). This construction, which was first found at the beginning of the century,[3] was recently rediscovered.[5]

Which part of the tree corresponds to the Fibonacci lattices that are seen in nature? We see in Fig. 1 that pairs of neighboring Fibonacci numbers lie along a continuous chain of branches, marked by crosses. Along this chain, the numbers increase monotonically. This observation suggests some process of growth or evolution of the lattice such that the lattice continually goes through a sequence of Fibonacci states. When we attempt to analyze this process on the basis of the disk model, we run into an obvious difficulty: We need to introduce some rules which specify the "desirable" directions to take at the branch points. The construction becomes rather contrived and not very attractive.

This difficulty can be avoided by working in an energy model.[6,7] We consider a lattice on a plane specified by the two parameters x,y:

$$\vec{r}_{mn} = ((m+nx)/\sqrt{y},\ n\sqrt{y}), \qquad m,\ n \in Z. \tag{2}$$

Lattice (2) is found from lattice (1) by rolling out the cylinder into a plane and by reducing the scale by a factor of $2\pi\sqrt{y}$ ($h = 2\pi y$, $\alpha = 2\pi x$). We define the energy $E(x,y)$ of this lattice as the sum of the energies of the interactions of nodes in pairs:

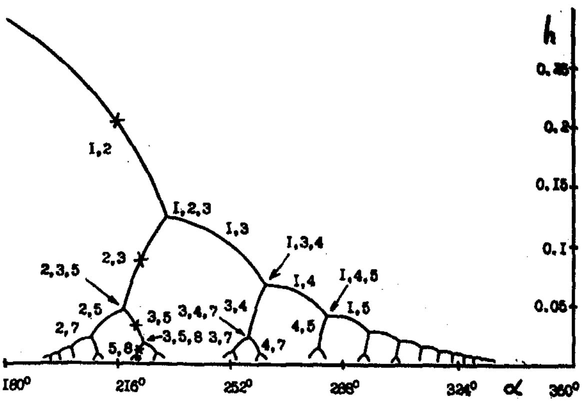

FIG. 1. A set of pairs α, h corresponding to lattices which are formed on a cylinder by identical touching disks.[3] The integers are the numbers of spirals formed by rows of nearest neighbors. The arcs marked with crosses correspond to Fibonacci lattices. The pattern is symmetric under the substitution $\alpha \to 360°-\alpha$, so only the region $\alpha > 180°$ is shown (the same comments apply to Figs. 2 and 3).

$$E(x,y)=\sum_{mn} U(|r_{mn}|). \quad (3)$$

The interaction $U(\lambda)$ can be any repulsive interaction; for our calculations we will adopt $U(\lambda)=\exp(-\lambda^2)$.

We now consider the following process. We deform lattice (2) by reducing y from $+\infty$ to 0, while leaving the parameter x free, allowing the lattice itself to choose the value of x at the minimum of the energy $E(x,y)$ for the given y. Let us examine the trajectories of minima $x_{\min}(y)$ which are found. In other words, we take all pairs (x,y) corresponding to local minima of E with respect to x under the condition $y=$ const, and we draw them on the x–y plane. We obtain a set, as shown in Fig. 2. We see that the number of minima of E with respect to x increases with decreasing y. A point of importance for our purposes is that the new minima appear in positions isolated from the old minima. This result means that by reducing y and following the minimum on the basis of continuity we will never run into an ambiguity regarding the continuation of the path, in contrast with the disk model. The reason why the new minima are isolated from the old ones lies in the asymmetry of the potential $E(x)_{y=\text{const}}$. Each new minimum appears not as the result of an exact bifurcation but through a "quasibifurcation," i.e., it is already at a nonzero distance from an old minimum when it first appears. Starting at some sufficiently large value of y, say $y=0.2$, and then reducing this value, we obtain a Fibonacci sequence of lattices in a deterministic manner. We go through the entire sequence, from its beginning to arbitrarily large Fibonacci numbers (cf. Fig. 1).

The relationship of the tree structures in Figs. 1 and 2 with each other can be described by associating both with Farey hierarchies of rational numbers.[8] The Farey construction runs as follows: We define the Farey sum of rational numbers: $m/n\oplus p/q=(m+p)/(n+q)$. We write 0 and 1 as 0/1 and 1/1; adding, we find $0/1\oplus 1/1=1/2$. We write 1/2 between 0/1 and 1/1, obtaining 0/1, 1/2, 1/1. We again add

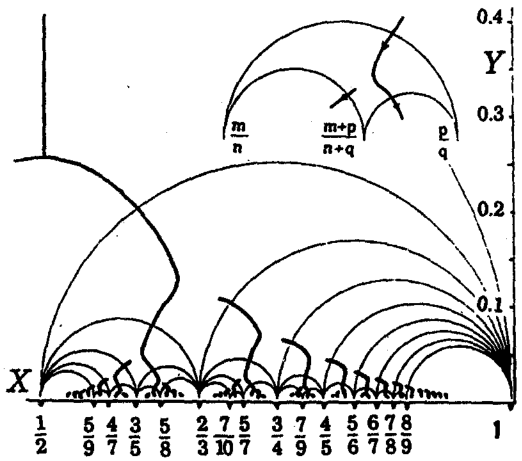

FIG. 2. Heavy lines—Trajectories of minima of E with respect to x under the condition $y=$ const; thin lines—semicircles which partition the region $y>0$ into curvilinear triangles, within which the behavior of the trajectories is the same. The inset shows the trajectories of minima in one triangle.

neighbors, and we write the results in between existing terms: 0/2, 1/3, 1/2, 2/3, 1/1. We continue in this manner. As a result of these calculations, we obtain all the rational numbers between 0 and 1, organized hierarchically. Each number appears exactly once. We arrange these numbers in different levels, in accordance with the levels of the Farey process at which they appear. We connect each number with the two "ancestors" whose sum gives the number, using a heavy line to the "younger" ancestor and a dashed line to the "older" one (Fig. 3). (The "older" ancestor is at a level higher than that of the "younger" one.)

It is not difficult to see that the topology of the resulting system of heavy lines in Fig. 3 is the same as the trajectories of minima in Fig. 2. This assertion can be proved rigorously in the following formulation.[7] We draw all possible circular arcs constructed on segments $(m/n,\ p/q)$ of the real axis, used as diameters (m, n, p, and q are integers; $mq - np = \pm 1$). We find that the half-plane $y > 0$ is thereby partitioned into curvilinear triangles with vertices m/n, $(m+p)/(n+q)$, p/q, as shown in Fig. 2. It turns out that the behavior of the trajectories of minima in all these triangles is the same: One trajectory goes into a triangle from above, crossing the long side, and leaves at the bottom, crossing the smaller side. Another trajectory appears, isolated, inside the triangle and exits downward across the intermediate side (see the inset in Fig. 2). It turns out that the entire pattern of trajectories of minima in Fig. 2 consists of standard blocks: triangles with vertices m/n, $(m+p)/(n+q)$, p/q. We thus have relationships with a Cayley tree (Fig. 1) and a Farey hierarchy (Fig. 3) simultaneously.

This process of deformation of the lattice (a smooth decrease in y with an appropriate adjustment of x) has a simple biological meaning. Let us imagine that the embryo of a pine cone forms as a one-dimensional structure through a sequential accumulation of seed embryos, head to tail. We obtain a chain of embryos: a long, thin object with a large length-to-thickness ratio. An embryo then grows and converts into a mature cone, and the length-to-thickness ratio decreases to its usual value. The growth is thus anisotropic: relatively fast in the transverse direction and relatively slow in the longitudinal direction. Aside from the general change of scale during the

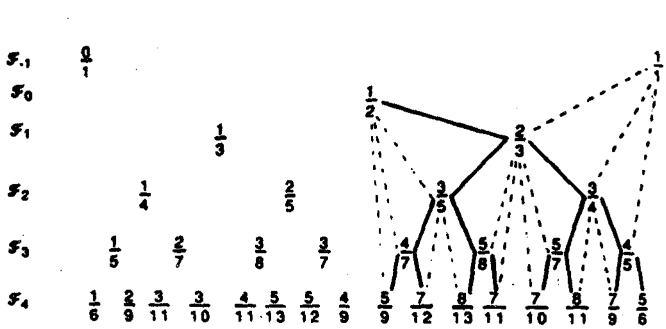

FIG. 3. Rational numbers from 0 to 1 organized hierarchically with the help of a Farey process.

growth, this process corresponds precisely to a decrease in our parameter y: the ratio of the vertical scale of the lattice to the horizontal scale. Consequently, because of purely mechanical factors, only Fibonacci structures form during the anisotropic growth of a long, cylindrical embryo.

It can be shown[7] that the topology of the trajectories of minima in Fig. 2 is stable with respect to changes in the repulsive potential U. This stability explains the universality of phyllotaxis and its widespread occurrence in the plant kingdom. We might add that our model in (2), (3) also applies to another problem: the vortex lattices in layered superconductors,[6] in which Fibonacci lattices again play a special role.

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