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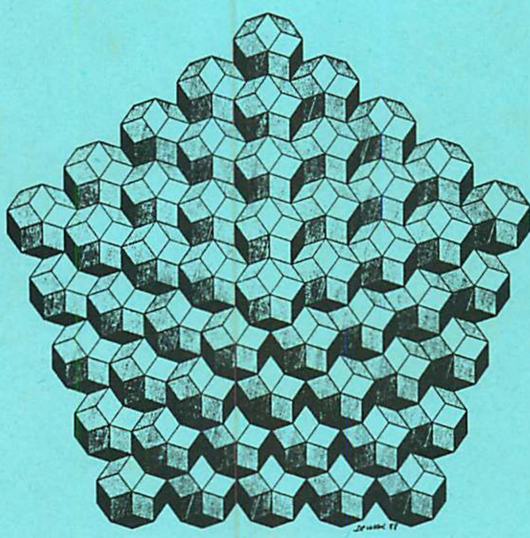
Abstracts

I.



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A GROWTH MODEL OF PHYLLOTAXIS:
The Dynamics That Produce a Living Crystal

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1. The Subject. Phyllotaxis is the study of the patterns formed by leaves, scales or florets on a plant. A phyllotactic pattern is like a living crystal.

2. Preliminary Facts and Concepts, Mathematical and Botanical.

A. A generalized Fibonacci sequence is determined by its first two terms a_1, and a_2 (which may be any two integers), and the recurrence relation $a_{n+1}=a_n+a_{n-1}$, $(n>1)$, which generates the rest. Sequences that play an important role in phyllotaxis are those whose first two terms are 1, t, with $t>0$, and t, 2t+1, with $t>1$. Examples of the first type are (F_n)=1, 2, 3, 5, 8, 13,... (usually called the Fibonacci sequence because it was the first one ever studied), and 1, 3, 4, 7, 11, 18, ... (known as the Lucas sequence). An example of the second type is 2, 5, 7, 12, 19, ...

B. The golden section g is the positive root of the equation $x^2=x+1$. $g=(1+\sqrt{5})/2$.

C. On a mature stem, if there is only one leaf at each node (level on the stem), they all lie on a helix known as the genetic spiral .Since the size of a stem does not appear to be relevant, we exclude it as a factor by picturing the stem as a normalized cylinder whose girth is taken as the unit of measure. Leaves are numbered in the order of their emergence, starting with 0. The internode distance between leaves i-1 and i is designated by r_i, and is called the rise. The angle of rotation around the axis of the cylinder between leaves i-1 and i expressed as a fraction of a turn is designated by d_i and is called the divergence.

(Fig. 1. Normalized cylindrical representation)

D. The picture looks different when the units (leaves, scales or florets) are crowded, as on the growing tip of a stem, or on a pineapple, pine cone, or sunflower head. What is observed then are two sets of conspicuous spirals called parastichies. One set goes up to the left, and the other set goes up to the right. If there are m left parastichies and n right parastichies, we say that the plant has (m,n) phyllotaxis. The conspicuous parastichies are determined by joining each unit to its nearest neighbor on the left and on the right. They are secondary spirals determined by the genetic spirals that are themselves not conspicuous. It can be shown that if the phyllotaxis is (m,n), the number of genetic spirals is the greatest common divisor of m and n. Consequently, in the case of a single genetic spiral m and n are relatively prime.

E. The phenomenon of phyllotaxis occurs on many different kinds of surface. We convert them all into normalized cylinders by means of appropriate conformal transformations.

F. A plastochrone is the length of time between the emergence of any unit i and its successor i+1. Time T is measured in plastochrones starting with the emergence of unit 0.

3. The Principal Facts of Phyllotaxis. a) As the number of units increases, there is a period during which the phyllotaxis (m,n) rises to higher and higher values, that is, with higher values of m and n. b) During this period of increasing phyllotaxis, (m,n) with m<n is succeeded by (m+n,n). c) d_i converges rapidly to a limiting value. In nearly all cases of phylllotaxis (m,n), m and n are consecutive Fibonacci numbers, and the limit to which d_i converges is g^{-2}.

4. The Central Problem. What is the explanation for the three facts cited in paragraph 3?

5. Assumptions for the Growth Model.
1) Successive units arise at equal intervals on the genetic spiral, so that d_i and r_i are independent of i, hence have values d and r that are functions only of time T. 2) r(T) is a monotonic decreasing function of T that approaches 0 as a limit as T increases to infinity. 3) Beginning with some instant T_c, d(T) is such that the minimum distance between units is a maximum relative to the values of the minimum distance that correspond to neighboring values of d.

6. The Phase Space. With these assumptions, the state of a system of phyllotaxis is given by two parameters, d and r. The phase space then is the (d,r) plane, and the development of the phyllotaxis of a plant as time passes may be pictured as a path in the plane.

7. The Problem Solved. On the basis of these assumptions we obtain an explanation for each of the facts cited in paragraph 3: a) Rising phyllotaxis is a consequence of decreasing r. b) The addition rule which governs rising phyllotaxis, that is, that (m,n) phyllotaxis with m<n is succeeded by (m+n,n) phyllotaxis, is a consequence of the maximization of the minimum distance between units. c) If maximization of the minimum distance begins early, that is, before $r<\sqrt{3}/38$, or while T<5, then it is inevitable that in succeeding values of (m,n) phyllotaxis the m and n be consecutive Fibonacci numbers and the limiting value d of the divergence be g^{-2}.

8. Consequences of the Assumptions (Adler, 1977). Suppose that at time T_c units m and n are the units that are nearest to unit 0. Then the phyllotaxis is (m,n). We assume without loss of generality that m<n. Maximization of the minimum distance between units implies that dist(0,m)=dist(0,n). This equation is the equation of a circle in the (d,r) plane. Consequently, as T increases, the point that represents the state of the system descends along an arc of this circle until dist(0,m+n)=dist(0,n)=dist(0,m). After that the point that represents the state of the system descends along an arc of the circle whose equation is dist(0,m+n)=dist(0,n), and the phyllotaxis changes from (m,n) to (m+n,n). With further decrease in r, the state of the system switches from an arc of the circle dist(0,m+n)=dist(0,n) to an arc of the circle dist(0,m+n)=dist(0,m+2n), then to an arc of the circle dist(0,m+2n)=dist(0,2m+3n), etc. These successive arcs form a

connected zig-zag path with narrower and narrower swings to the right and left. The projections of these arcs on the d-axis form a nest of intervals, and the divergence d converges to the value of the point that is inside the nest.

(Fig 2. The Phyllotaxis Path)
(if maximization of the minimum distance begins early)

9. The Vortex Metaphor. Fig. 3 is a series of graphs of the square of the minimum distance between units as a function of d, each drawn for some fixed values of r and T. The graphs show that for high r and low T there is at first only one maximum. Then, as T increases and r decreases, more and more maxima appear. If maximization first occurs at some time T, any one of these maxima may be the starting point of the kind of zig-zag path just

(Fig. 3. The Square of the Minimum Distance as a Function of d)

described. It is as though there are many vortices in the (d,r) plane, with more and more of them present in the regions closer to the d-axis. When maximization of the minimum distance between units first occurs, the point (d,r) that represents the state of the system moves to the nearest vortex and then descends into it.

(Fig. 4. Vortices in the (d,r) Plane)

10. Weakening the Assumptions. The model described above used the very strong assumptions that d_i and r_i are independent of i. Weakening these assumptions does not affect the conclusions reached for the following reasons: 1) The argument can still be carried through using the average of the d_i as the value of d, and the average of the r_i as the value of r. 2) It can be proved that maximization of the minimum distance between units compels an equalization of the values of the d_i.

11. The Wave. Using reasonable equations for $r_i(T)$ for units on a parabolic surface or on a disc shows that as more and more units emerge, the younger ones recapitulate the history of older ones, that is, the values of d_i and r_i, as they change with increasing T, recapitulate the values that d_i and r_i passed through at an earlier time. This means that the vibration of d travels as a wave from the older to the younger units.

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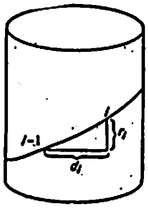

Fig. 1. Normalized Cylindrical Representation

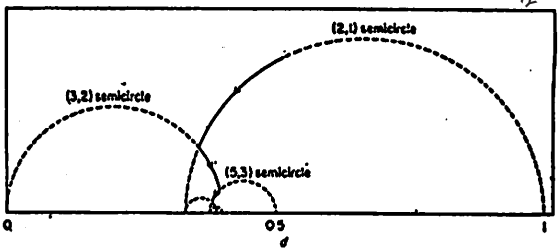

Fig. 2. The Phyllotaxis Path if maximization of the minimum distance begins early

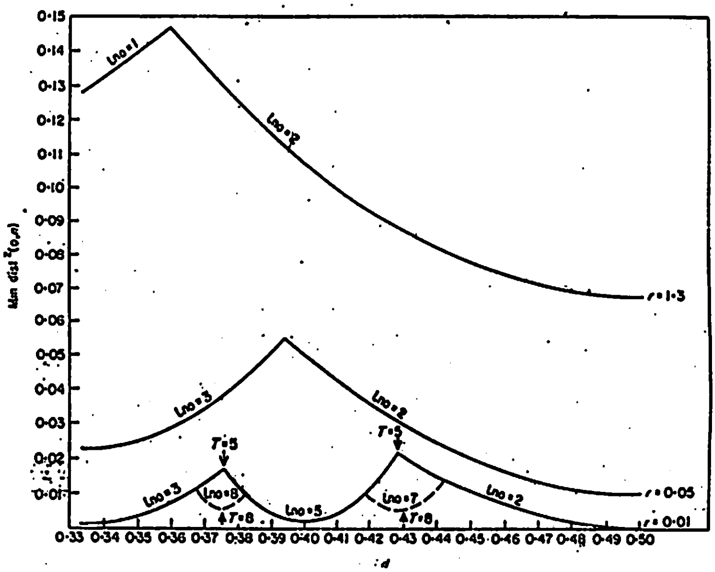

Fig. 3. min dist² (0, n) as a function of d when T = 5 and T = 8. (Lno = leaf nearest zero.)

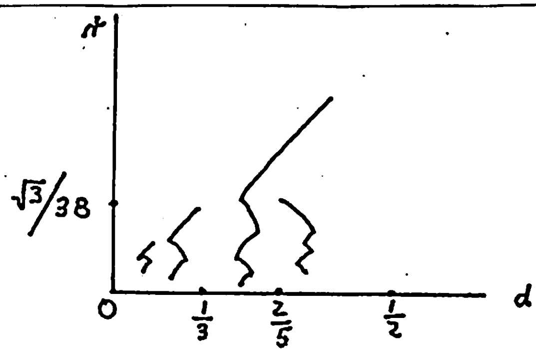

Fig. 4. Vortices in the (d,r) plane (Schematic diagram)