Symmetry: Culture

and Science
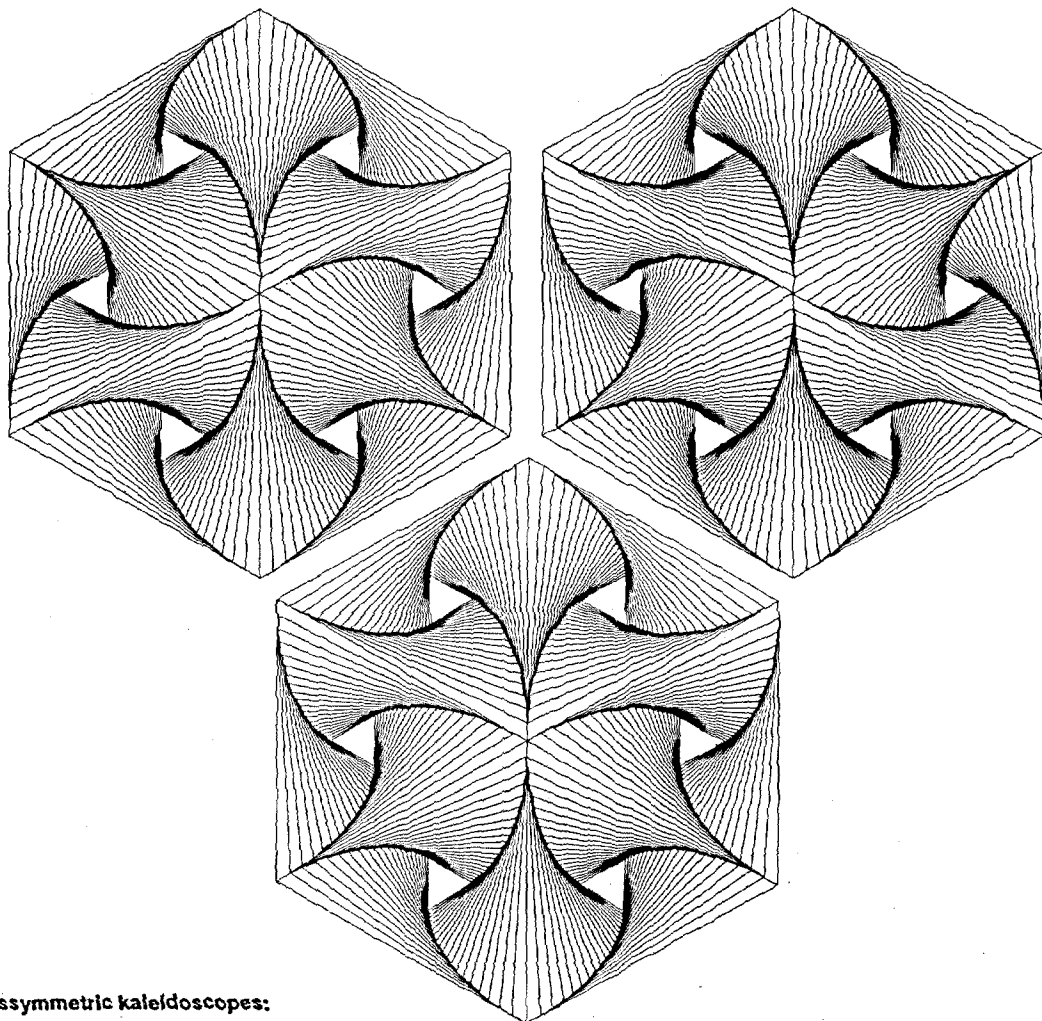
Dissymmetric kaleidoscopes:
Hommage à Pasteur

Symmetry

CULTURE & SCIENCE

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SYMMETRY: SCIENCE & CULTURE

SYMMETRY IN PHYLLOTAXIS

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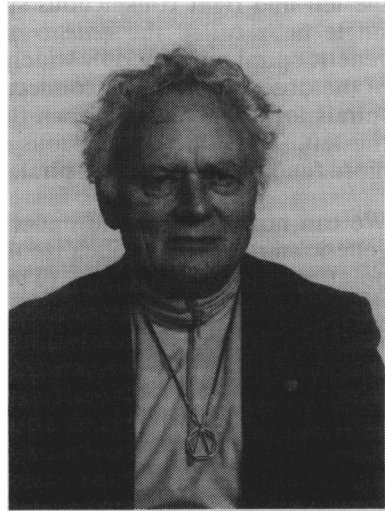
QUESTION 1
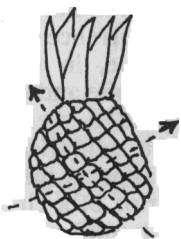
what is symmetry?

Figure 1: Conspicuous spirals on a pineapple.

On a pineapple farm near Brisbane, Australia there is a one-story building intended to look like a giant pineapple. It shows clearly that a pineapple is like a living crystal: the closely packed florets on its surface are arranged in two intersecting sets of parallel spirals. One set goes up to the right. The other set goes up to the left. The architect who designed the building was aware of the fact that there is symmetry in the arrangement of the florets, since he had put 13 spirals into each of the sets, and both sets of spirals made the same angle with the ground. However, the symmetry he gave his pineapple building is wrong. In a real pineapple, the two sets of conspicuous spirals *do not* have equal numbers of spirals. In a

(b) A brief note in *Nature* (Frey-Wissling, 1954) pointed out that divergence angles in a polypeptide chain are analogous to divergence angles in phyllotaxis, and can be derived from the sequence 1, 3, 4, 7, ... which is generated by the same recurrence relation as that which generates the Fibonacci sequence if you begin with 1, 3 instead of 1, 2. "The similarity", he said, "is certainly due to the same geometric cause, that is, as dense as possible an arrangement of identical objects along a helix". Erickson (1973) pursued this idea further and proposed the use of concepts and terminology of phyllotaxis to describe microscopic biological structures that are assembled from protein monomers in helical arrangements like those displayed by the close packing of equal spheres around a cylindrical surface. Using these concepts borrowed from phyllotaxis, he showed how the parameters of these structures can be calculated from observed data. He used two methods employing the notation and equations of Van Iterson (1907). The first method was based on using for the distance between the centers of two neighboring spheres the length of the straight line-segment that joins them. This method leads to transcendental equations that can be solved by an iterative procedure. In the second method, he used for the distance between the centers of two neighboring spheres the length of the helical arc that joins them on the cylindrical surface that contains them. This method leads to simple algebraic equations that are solved more directly than the transcendental equations of the first method and provides solutions that are close approximations to those obtained by the first method. The equations Erickson used in the second method, however, apply only to the triple-contact case (hexagonal packing). In 1977 I showed how this method could be made more general, so that it would be applicable to both the triple-contact case and the double-contact case (rhombic packing) (Adler, 1977b) by using the equations derived in my contact-pressure model of phyllotaxis (Adler 1974, 1977a).

(c) The study of phyllotaxis has had an important impact on the teaching of mathematics. Counting the spirals on a pineapple, a pine cone, or a sunflower , and discovering that the numbers obtained are consecutive terms of the Fibonacci sequence immediately arouses student interest in this sequence. As I have pointed out in talks to teachers in the United States, Australia, New Zealand, Hong Kong, Singapore, and Malaysia (Adler, 1984), introducing young people to the Fibonacci numbers opens the door to a host of mathematical concepts, with some suitable for every grade level. These numbers are joined by many threads to the rest of the fabric of modern mathematics. Here is a list of some of the subjects entered if the threads are followed: theory of limits, linear algebra (determinants and matrices, modules and vector spaces, spectral theory), theory of rings and fields, theory of numbers (Diophantine equations, congruences, continued fractions, theory of primes), differential equations, theory of linear recurrence relations, combinatorial analysis, and theory of functions of a complex variable.

The Fibonacci numbers also provide students with many opportunities to make their own discoveries. For example, even students in the elementary grades can discover for themselves the formula for the sum of the first *n* consecutive Fibonacci numbers, and the formula that, for any three consecutive Fibonacci numbers, connects the product of the first and third number to the square of the middle number.

decreases, this vertical component becomes negligible. Then a lattice point with a high lattice number can become the point nearest 0 if the horizontal component of its distance is small. If m and n are the lattice points nearest to 0 on the left and right respectively, then the opposed parastichy pair (m, n) is called *conspicuous*. It can be proved that a conspicuous opposed parastichy pair is necessarily visible (Adler, 1984, letter to Roger Jean). The significance of these distinctions is this: the divergence angle d determines which opposed parastichy pairs are visible, and vice versa, in a manner explained in the next paragraph, and, for a given value of d it is r that determines which visible opposed parastichy pair will be conspicuous.

To be able to explain the connection between the divergence angle d and the phyllotaxis (m, n) we must first introduce two more concepts. If (m, n) is a visible opposed parastichy pair and $m > n$, then $(m, n-m)$ is called its *contraction*. The contraction of a visible opposed parastichy pair is necessarily visible (Adler, 1974). It is important that *a contraction is not uniquely reversible*, contrary to what Tait assumed (Tait, 1872). If (m, n) is a visible opposed parastichy pair, then $(m+n,n)$ is called its left extension, and $(m, m+n)$ is called its right extension. In general, only one of these two extensions is visible, depending on what the value of the divergence angle d is: There is a certain maximal interval [a, b] in which d may be if (m, n) is visible. The median between a and b divides this interval into two segments. *The left extension of* (m, n) *is visible if and only if* d *is in the left segment, and the right extension is visible if and only if* d *is in the right segment.* The following propositions can be established : If the genetic spiral is a right spiral, every visible opposed parastichy pair (m, n) with $m, n > 1$ can be obtained as the end product of a sequence of extensions starting with a visible opposed parastichy pair of the form $(t, t+1)$, where t is a uniquely determined integer greater than 1. Moreover $(t, t+1)$ is visible if and only if d lies in the interval $[1/(t+1), 1/t]$. Now here is where the continued fraction for d becomes relevant. Since the terms of the continued fraction determine whether d is in the left segment or the right segment after each successive insertion of the median between the ends of the segment previously determined, they also determine whether the corresponding extension that is visible will be a left extension or a right extension. For example, $(2, 3)$ is visible if and only if d is in the interval $[1/3, 1/2]$. The median between $1/3$ and $1/2$ is $2/5$. $(5, 3)$ is visible if and only if d is in the interval $[1/3, 2/5]$. $(2, 5)$ is visible if and only if d is in the interval $[2/5, 1/2]$. Further visible extensions of a visible opposed parastichy pair go hand in hand with further restrictions of the range of d. The terms of the continued fraction choose in succession a left or right segment for the position of d as each of these segments is divided in turn by the median between its endpoints. To each segment there corresponds a visible opposed parastichy pair. The choice of left or right segment when the segment is divided by the median determines whether the left or right extension of the corresponding visible pair will also be visible. Since an opposed parastichy pair is conspicuous only if it is visible, the phyllotaxis of a stem is thus intrinsically tied to the value of d. (As already mentioned, it also depends on the value of r.)

The state of a system of phyllotaxis is determined by the two parameters d and r. It can therefore be represented by a point in the corresponding phase space, namely, the (d, r) plane. In my model of phyllotaxis it is assumed that r is a decreasing function of time. Then the changes the system undergoes with the passage of time are pictured as the path this point follows as r decreases. In my model I show that if the minimum distance between units is maximized, then if m and n are the units

typical pineapple, the two numbers are 8 and 13, not 13 and 13, and the angles they make with the base are not the same. The symmetry displayed by a pineapple is an *asymmetrical symmetry*.

To describe this symmetry we first idealize the picture by assuming the surface of the pineapple to be cylindrical, and we think of each of the conspicuous spirals as a helix drawn on the cylinder. A rotation of 360°/13 will bring the set of 13 spirals into coincidence with itself, and a rotation of 360°/8 will bring the set of 8 spirals into coincidence with itself. But neither of these rotations will bring both sets of spirals into coincidence with themselves. Moreover, while each of these rotations brings one of the sets of spirals into coincidence with itself, it does not necessarily bring the set of florets on them into coincidence with itself. To find a motion that will do this we have to uncover a more fundamental feature of the arrangement of the florets. The numbers 8 and 13 are relatively prime. Whenever the numbers of the left and right conspicuous spirals are relatively prime, the florets all lie on a single helix called the *genetic spiral* (Bravais, 1837). Consecutive florets on the genetic spiral are generally widely separated horizontally on the surface, so the eye of the observer does not connect them. Instead, the eye observes the conspicuous spirals formed by joining each floret to its nearest neighbors on the right and on the left. Thus, the conspicuous spirals are secondary spirals associated with the more fundamental genetic spiral.

We can now describe the underlying symmetry of the pineapple in terms of the genetic spiral. First we idealize the picture further by representing each floret by a point on the genetic spiral. (Think of it as the center of the floret.) The picture then
becomes that of a point-lattice on a cylinder. The florets are arranged at equal distances on the genetic spiral. To bring a floret into coincidence with the next higher floret, it suffices to turn the surface around its axis through an angle, called the *divergence angle*, and then move the surface in a direction parallel to its axis through a distance called the *internode distance*. It is useful in the theory to normalize the surface by taking its girth as the unit of measure. In the normalized surface the divergence angle, expressed as a fraction of a turn, is numerically equal to the length of the horizontal component of the distance between consecutive florets on the genetic spiral, and is designated by d. The internode distance in the normalized surface is called the *rise* and is designated by r.
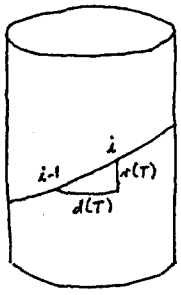
The phenomenon of units arranged in two sets of conspicuous spirals displayed by the florets of a pineapple is a common occurrence in plants. It appears also, for example, in the arrangement of the scales of a pine cone and in the arrangement of leaves around a stem. Moreover, it is not restricted to a cylindrical surface. The surface on which it appears may be approximately a disc (the interior of a circle), as on the head of a sunflower, or a parabolic surface, as at the growing tip of a stem where the embryo leaves emerge. By an appropriate conformal transformation each of

Figure 2: The genetic spiral on a normalized cylinder (girth =1).

is surely manifest that the simple way to do so is to elongate the axis, and to set the leaves farther apart, lengthways on the stem. This has at once a far more potent effect than any nice manipulation of the 'angle of divergence'." Airy (1873), whose paper was presented to the Royal Society by Charles Darwin, also claimed that natural selection explained the spiral arrangement of leaves, but gave a different explanation of what it was selecting for. The usefulness of the Fibonacci pattern of phyllotaxis, he said, was found, not in the mature stem, where the leaves are widely separated, but in the bud, where the embryo leaves are closely packed: "In the *bud* we see at once what must be the use of leaf-order. It is for *economy of space*, whereby the bud is enabled to retire into itself and present the least surface to outward danger and vicissitudes of temperature."

Schwendener, influenced by the obvious successes of mechanics in physics, put forward a mechanical theory of leaf arrangement (1878) in which the convergence of the divergence angle to g^{-2} was explained by the contact pressure that leaf primordia exert on each other. Unfortunately, his mechanical transposition to botany of concepts derived from mechanics didn't succeed because his argument based on a force diagram was fallacious (see Adler, 1977a, p. 50).

Meanwhile a new branch of physics was coming to the fore, namely, thermodynamics. In this branch, attention was centered on the flow of energy, rather than on force diagrams. In the new intellectual climate created by thermodynamics, Church developed his theory that is based on assumed pulses of energy. He rejected the idea of a genetic spiral, and insisted instead that the parastichies are fundamental. Using the disc picture you get when you take a cross-section of the growing tip of a stem, he said that impulses of energy travel away from the center of the disc in spiral paths, and that new leaves emerge where the spirals intersect (Church, 1904, 1920). While his theory uses terminology borrowed from physics, it clearly reflects the influence of the *vitalist* school of thought in biology.

Meanwhile attention in biology was shifting from anatomy and histology to biochemistry. In this new climate of thought Schoute (1913) advanced the hypothesis that the initial position of a leaf primordium is determined by the action of an inhibitor secreted by the primordia already present. The inhibitor prevents another primordium from emerging too close, and the location of a new primordium is determined by the inhibition emanating from the two nearest primordia already growing. Whether such an inhibitor exists is still an open question.

My own thinking which led to the construction of a mathematical model for a contact-pressure theory of phyllotaxis was influenced by the philosophy of dialectical materialism. Because of my materialist outlook, I sought an explanation in terms of cause and effect. Because of my dialectical outlook, I looked for the internal contradiction in the dynamics of growth of a stem that might provide a clue to what happens. I found this contradiction in the fact that, as Schimper (1830, p. 25) had pointed out, while leaf primordia tend to separate as far as possible, they are also constrained to grow toward each other. Neighboring primordia grow toward each other until they make contact. After that, further growth compels their centers to move apart. But, since they are confined to a finite space, the distance between them ultimately becomes maximized. The essential content of my model is the rigorous determination of the consequences of the maximization of the minimum distance between primordia (Adler, 1977a).

(a) Ever since the first systematic study of phyllotaxis was undertaken by Schimper (1830), Braun (1831, 1835) and the Bravais brothers (1837), the divergence angle has been represented by its expansion as a simple continued fraction. While investigating the connection between the divergence angle d and the numbers of conspicuous secondary spirals (m, n), I uncovered the geometrical meaning of a simple continued fraction: *it represents a mediant nest of intervals* (Adler, 1978). As is well known, for any given nest of intervals on the real line $i_1, i_2, ..., i_n, ...$, where each i_n is wholly contained in i_{n-1}, and where the length of i_n approaches zero as n approaches infinity, there is a unique real number that lies in all the intervals of the nest. A mediant nest is a special kind of nest constructed as follows with the help of the concept of the mediant between two rational numbers. If a/b and c/d are rational numbers in lowest terms, then the fraction $(a+c)/(b+d)$ is called their mediant. It is easily seen that it lies between them, and that it, too, is in lowest terms. Now begin with the positive half of the real line, and represent 0 by the fraction $0/1$, and represent infinity by the fraction $1/0$. The mediant between them is $1/1=1$. This point divides the positive half of the real line into two intervals: the left interval is between 0 and 1; the right interval is between 1 and infinity. Choose one of these intervals as i_1, and represent your choice by either 0 or 1, according as you chose the left or right interval respectively. Then in the interval you chose, insert the mediant between its endpoints, dividing it into two intervals. Choose one of them as i_2 and represent your choice by 0 if you chose the left interval and by 1 if you chose the right interval. Continue in this way ad infinitum to obtain a nest of intervals $i_1, i_2, ..., i_n, ...$ represented by a sequence of zeros and ones. The zeros and ones in the sequence occur in clusters, with each cluster of ones ending where a cluster of zeros begins, and vice versa. Let a_1 be the number of ones in the first cluster. (It may be zero or a positive integer.) Let a_2 be the number of zeros in the next cluster, let a_3 be the number of ones in the next cluster, etc, so that a_n is a number of zeros if n is even, and is a number of ones if n is odd. Then the number defined by the mediant nest is the number represented by the simple continued fraction $a_1 + 1/a_2 + 1/a_3 + ... + 1/a_n + ...$ (in this notation we use the convention that everything that follows a fraction line / is understood to be under it). Thus every simple continued fraction can be interpreted as a set of instructions for constructing a mediant nest that contains the number that the simple continued fraction represents: begin with the positive half of the real line, and insert mediants as described above. Then construct the mediant nest by first choosing the right interval a_1 times, then choosing the left interval a_2 times, then choosing the right interval a_3 times, etc. The mediant nest associated with the simple continued fraction that represents the divergence angle d plays a significant role, as we shall see, in the connection between d and the phyllotaxis (m, n).

D'Arcy Thompson, in his famous book *On Growth and Form* (1942), after discussing the secondary spirals seen in phyllotaxis, said: "The determination of the precise angle of divergence of two consecutive leaves of the generating spiral does not enter into the above general investigation [...], and the very fact that it does not so enter shews it to be essentially unimportant." This conclusion is entirely wrong. Before the real connection between the divergence angle d and the phyllotaxis (m, n) could be established it was first necessary to make some precise distinctions among different kinds of secondary spirals. Botanists use the term *parastichies* for secondary spirals, so we shall use this term from now on. Although the terminology