

The Role of Continued Fractions in Phyllotaxis

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1. INTRODUCTION

Phyllotaxis is the study of the arrangement of botanical units such as leaves, scales, and florets around a stem. From the very beginning of the scientific study of this subject (in 1830; see (12)) the numbers observed in phyllotaxis were seen to be connected to simple continued fractions. The reason for this connection, however, was not immediately understood. Because of this, one leading botanist (see Section 8) rejected it outright as meaningless playing with numbers, and one well-known mathematician (see Section 7) was trapped into an erroneous argument leading to a false conclusion. It was not until 1974 that the real connection between continued fractions and the numbers significant in phyllotaxis was finally clarified in a few rigorously established theorems about cylindrical point-lattices. But first it was necessary to clarify the concepts that arise in phyllotaxis. This is the subject of Section 9. It was also necessary to seek out the underlying geometric meaning of a simple continued fraction. This is taken up in Section 12. The rest of this paper traces the history of the connection between phyllotaxis and continued fractions from the time it was first observed to the time it was finally understood.

2. BASIC CONCEPTS

The first detailed studies of phyllotaxis, performed by Schimper (12) and Braun (4, 5), were restricted at first to the arrangement of leaves around a mature stem and were then extended by Braun to the patterns formed by

the scales of a pine cone. These studies introduced several basic concepts:

DEFINITION. In the case where there is at most one leaf at any level on the stem the leaves may be pictured as points at equal intervals on a helix wound around a cylinder (Fig. 1). This helix is called the *fundamental* or *genetic spiral*.

DEFINITION. A series of consecutive leaves forms a *cycle* if the highest leaf in the series is the first one to be directly over the lowest leaf.

Schimper and Braun assumed to begin with that such a cycle always exists.

DEFINITION. The fraction of a turn between consecutive leaves in a cycle is called the *divergence*, and is designated by d .

When d is rational, as Schimper and Braun assumed it would be, it is equal to the fraction p/q , where p is the number of times the helix winds around the cylinder between the top and bottom of the cycle, and q is the number of intervals between consecutive leaves in the cycle.

Schimper and Braun took note of the fact that there are two different fundamental spirals that can be drawn for the same set of leaves, one joining them the short way around the stem and one joining them the

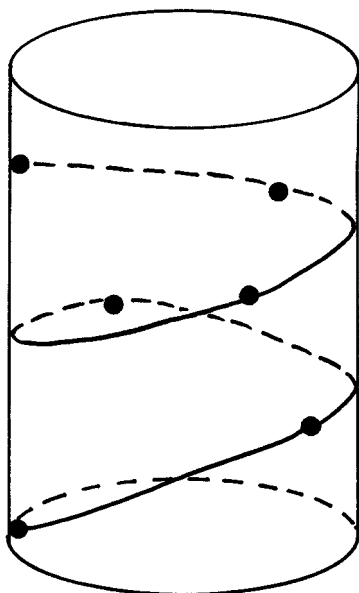


FIG. 1. A cycle with five intervals in two turns: divergence = $2/5$.

other way around. If the short way around is chosen, then the divergence is $\leq \frac{1}{2}$. The divergence, Braun asserted, determines all other properties of a leaf arrangement. This assertion turns out to be incorrect. Another number, the *rise*, designated by r and defined in Section 9, is also relevant.

3. THE FIBONACCI NUMBERS, THE GOLDEN SECTION, AND CONTINUED FRACTIONS ENTER THE PICTURE

In their observations of many plants, Schimper and Braun found that in the most common divergences p/q , p and q were terms of the Fibonacci sequence $\{F_n\}$ defined by the recurrence relation $F_{n+2} = F_n + F_{n+1}$ and the initial condition $F_1 = F_2 = 1$. For the short way around, the typical divergence has the form F_n/F_{n+2} . For the long way around, the divergence is F_{n+1}/F_{n+2} . Braun (5) observed that these fractions are related to certain continued fractions. The divergences measured the long way around are the convergents of the continued fraction

$$\frac{1}{1 + \frac{1}{1 + \dots}}$$

and the divergences measured the short way around are the convergents of the continued fraction

$$\frac{1}{2 + \frac{1}{1 + \dots}}.$$

In both fractions all terms after the first are equal to 1. The latter fraction converges to $1/(2 + \tau^{-1}) = \tau^{-2}$, where τ is the golden section, $(1 + \sqrt{5})/2$. They also noted that some divergences that occur less frequently are convergents of the continued fraction in which 2 is replaced by $t > 2$. Such a fraction converges to $1/(t + \tau^{-1})$. Thus, with these early observations, continued fractions entered into the study of phyllotaxis. To explain their intrusion into the subject, Braun said that nature preferred these particular continued fractions as a source of divergences because they were the simplest, in that all terms after the first were equal to 1.

His intuition that continued fractions were relevant turned out to be correct, as we shall see. The fact that all terms after the first are equal to 1 did, indeed, turn out to be significant, but his explanation did not really explain anything.

4. CONFUSION IN TERMINOLOGY

By assuming the existence of cycles, where the top leaf is directly above the lowest leaf, Schimper and Braun assumed that a divergence is always a rational number, that is, a number that can be expressed as the ratio of two whole numbers. But they also knew that this assumption was not always correct, so that the rational numbers they used as divergences could only be approximations. Moreover, they introduced some confusion by their use of the terms *rational* and *irrational*. Braun used the term *rational* to refer to unit fractions such as $\frac{1}{2}$ and $\frac{1}{3}$, and used the term *irrational* for all other fractions. However, in standard mathematical usage, *all fractions* are rational numbers, and irrational numbers are those that *cannot* be expressed as fractions. Because of this confusion of terminology he may have thought that he was taking irrational divergences into account.

5. BRAUN'S METHOD FOR CALCULATING d

The fundamental spiral is not always easy to see. In that case Braun said that the divergence can be calculated by using the orthostichies and parastichies that can be seen.

DEFINITION. *Orthostichies* are vertical alignments of the leaves.

DEFINITION. *Parastichies* are secondary spirals determined by joining leaves to other leaves that are not necessarily their neighbors on the genetic spiral.

The denominator q of the divergence p/q is the number of orthostichies. To obtain the numerator, p , he noted first that parastichies that cross each other form parallelograms. Starting with parastichies that have the least inclination to the horizontal, he drew the diagonals of the parallelograms that they are part of. These diagonals are part of a set of steeper parastichies. He next used these to form parallelograms whose diagonals yield still steeper parastichies. Continuing in this way, a chain of diagonals is formed the last of which is vertical. The number of diagonals in this chain yields the desired numerator p . Obviously this method of calculating the divergence works only if orthostichies are present, and they are present only if the divergence is rational.

This method is therefore not completely general. The general rule that connects the parastichies to the divergence was first discovered in 1974 and is described in Section 10. There are usually two sets of parallel parastichies that catch the eye. One set goes up to the left, and the other goes up to the right. The numbers of parastichies in these two sets are

usually consecutive terms of the Fibonacci sequence. This is a second way in which the Fibonacci sequence enters into the study of phyllotaxis.

6. ADVANCES BY THE BRAVAIS BROTHERS

The Bravais brothers (6) were familiar with the work of Schimper and Braun, and referred to them frequently in their paper either by name or as "the German botanists." They, too, connected the most frequently observed divergences to the Fibonacci sequence and the continued fraction expansion for τ^{-2} . They argued, however, that the rational numbers cited by Schimper and Braun were not separate, distinct divergences, but only approximations to the one real divergence represented by the non-terminating continued fraction, namely the number τ^{-2} . Since then, botanists and mathematicians studying phyllotaxis have interpreted this in two different ways. Some assume that in the initial placement of leaves on the genetic spiral, they are already separated from each other by a divergence equal to τ^{-2} . Others, including this author, assume that other initial divergences are possible, but that there is a process occurring as the plant grows that causes the divergence to converge toward τ^{-2} as a limit.

The Bravais brothers used some techniques that have proved to be of lasting value in the further study of this subject. Picturing the plant stem as a cylinder and the leaves as points located at equal intervals on a helix, as did Schimper and Braun, they then introduced the plane development of the cylinder. This converts the genetic spiral and all parastichies into straight lines, and thus simplifies considerably the mathematics needed to describe the properties of the point-lattice. They numbered the leaves on the genetic spiral in the order of their appearance, making it possible to express phyllotactic relationships numerically. They also proved that if "the most easily seen" parastichies consist of m parallel spirals in one direction and n spirals in the opposite direction, then there is a single genetic spiral if and only if m and n are relatively prime. A refinement of the idea of what is "most easily seen" turns out to be necessary, and is taken up in Section 9.

7. A FALLACIOUS ARGUMENT BY TAIT

Tait (13), having seen the Bravais paper, decided that its elaborate arguments and calculations were superfluous. He offered what he considered to be a simple and complete solution to the puzzle of why the Fibonacci sequence seems to play a special role in phyllotaxis. If m parastichies are seen to go up to the left, and n parastichies go up to the

right, with $m > n$ and m and n relatively prime, then there may also be seen a set of $m - n$ less steep parastichies going up to the left, also crossed by the n parastichies going up to the right. Continuing the process of subtracting the smaller number from the larger, one ultimately arrives at a single parastichy in one direction with some number t parastichies in the other direction. (This follows from the fact that m and n are relatively prime.) The single parastichy is the genetic spiral, and a single turn of it contains t but not $t + 1$ leaves. In the most common case, $t = 2$, and the divergence is necessarily $> \frac{1}{3}$ and $\leq \frac{1}{2}$. This will occur, for example, if you start with two consecutive Fibonacci numbers, say 8 and 13. The pairs obtained by the subtraction process that he proposes would be 8 and 5; then 3 and 5; then 3 and 2; and finally 1 and 2. He then imagines his subtraction procedure reversed, and concludes that whenever the divergence is between $\frac{1}{3}$ and $\frac{1}{2}$ the values of m and n for the most conspicuous spirals must be consecutive terms of the Fibonacci sequence. The fallacy of his argument is exposed in Section 10. Thompson (14), assuming that Tait's argument was valid, concluded that "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 shows it to be essentially unimportant." This conclusion is the direct opposite of the statement by Braun cited at the end of Section 2. In Section 10, where we will state precisely how parastichy numbers are related to the divergence, we shall see that Thompson's conclusion is wrong.

8. SACHS REJECTS CONTINUED FRACTIONS AS NOT RELEVANT

Sachs (11), in his *Text Book of Botany*, pointed out that the continued fraction for $1/(2 + \tau^{-1})$ does not suffice to represent all divergences that are found in plants. Some are represented by the continued fraction for $1/(t + \tau^{-1})$, with $t > 2$. For this reason he concluded that "it seems to me absolutely impossible to imagine what value the method can have for a deeper insight into the laws of phyllotaxis." His reasoning here is faulty. He was ignoring the experience of physicists that in determining the laws governing a phenomenon two things are needed: a general rule, expressed in physics as a differential equation, and boundary conditions. In phyllotaxis the continued fraction for $1/(t + \tau^{-1})$ might well express a general rule, while the different values of t are the result of different boundary conditions. (See Sections 10-12.)

9. SOME NECESSARY DISTINCTIONS

The first step toward determining the exact role of continued fractions in phyllotaxis is discovering the precise connection between parastichy numbers and the divergence. But before this can be done it is necessary to introduce some distinctions among parastichies. For this purpose we begin with a cylindrical point-lattice with a single fundamental spiral going up to the right, numbering the lattice-points on this spiral $0, 1, 2, 3, \dots$. Experience shows that the phenomena of phyllotaxis are independent of scale. To eliminate scale as a factor, we normalize the cylinder by taking the girth of the cylinder as unit of length. Let $0L$ be the element of the cylinder through leaf 0 . Unroll the cylinder on a plane. Then the entire cylindrical lattice lies in a strip between two parallel lines, $0L$ and a copy of it, 0_1L_1 . By repeating this strip over and over again to the left and right and extending the genetic spiral downward, we convert the cylindrical point-lattice into a point-lattice in the plane (Fig. 2). Note that it contains many copies of 0 , designated respectively as $0_1, 0_2, 0_3$, etc. In this picture, the divergence, d , of the genetic spiral is the horizontal component of the distance between two consecutive leaves on it.

DEFINITION. The vertical component of the distance between two consecutive leaves on the genetic spiral on a normalized cylinder is called the *rise* and is designated by r .

(For a leaf distribution on a cylinder that is not normalized, the rise is the ratio of the internode distance to the girth of the cylinder.)

Let n be a leaf to the right of $0L$ whose distance from $0L$ is $\leq \frac{1}{2}$ and for which there is no leaf between 0 and n on the line that joins them. This line is a *right parastichy*; that is, it goes up to the right. It contains all those leaves and only those whose leaf numbers are multiples of n . Parallel to it are other parastichies, each containing the leaves belonging to a residue class modulo n . Thus the leaf n determines a set of n right parastichies. Similarly, a leaf m to the left of 0_1L_1 whose distance from 0_1L_1 is $\leq \frac{1}{2}$ and for which there is no leaf between 0_1 and m on the line that joins them determines a set of m left parastichies.

DEFINITION. The m left parastichies and n right parastichies constitute an *opposed parastichy pair* and are designated by the ordered pair (m, n) .

The m left parastichies cross the n right parastichies but, in general, there need not be a leaf at each of the intersections.

DEFINITION. In the special case where there is a leaf at every intersection of an opposed parastichy pair, we call it a *visible opposed parastichy pair*.

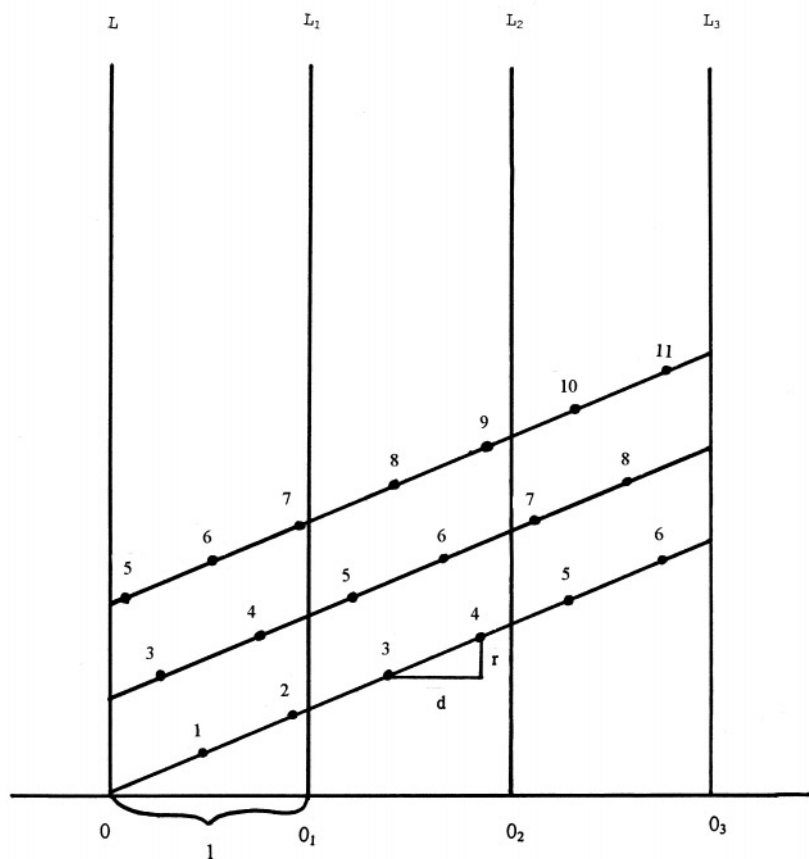


FIG. 2. Plane development of a normalized cylindrical point-lattice.

These are the pairs that are relevant to our investigation. That they play a special role had already been recognized by Van Iterson (15) who called them "konjugierte spiralen."

We have one more definition to introduce:

DEFINITION. If m and n are the leaves nearest to leaf 0 on the left and right, respectively, we call the opposed parastichy pair (m, n) *conspicuous*.

It is easily proved that a conspicuous opposed parastichy pair is a visible opposed parastichy pair. When botanists say that a leaf distribution has (m, n) phyllotaxis, they mean that (m, n) is a conspicuous opposed parastichy pair.

10. THE OPPOSED PARASTICHY TRIANGLE

We associate with any given opposed parastichy pair (m, n) a triangle constructed as follows: Extend the right parastichy determined by 0 and n to the lattice point mn . Then, from mn , draw downward the left parastichy determined by $0m$ that passes through it. This left parastichy will pass through some image 0_i of 0 .

DEFINITION. We call the triangle whose vertices are 0 , 0_i , and mn the opposed parastichy triangle belonging to (m, n) .

The length of its base, 00_i is i . The following proposition is easily proved:

PROPOSITION 1. *An opposed parastichy pair is a visible opposed parastichy pair if and only if the base of its opposed parastichy triangle has length 1.*

We now introduce the concept of *contraction* that was used by Tait without defining it precisely.

DEFINITION. If (m, n) is a visible opposed parastichy pair with $m > n$, then $(m - n, n)$ is its *contraction*. If $n > m$, then $(m, n - m)$ is its *contraction*.

Then, using Proposition 1 and the elementary properties of a plane point-lattice, we can prove:

PROPOSITION 2. *The contraction of a visible opposed parastichy pair is a visible opposed parastichy pair.*

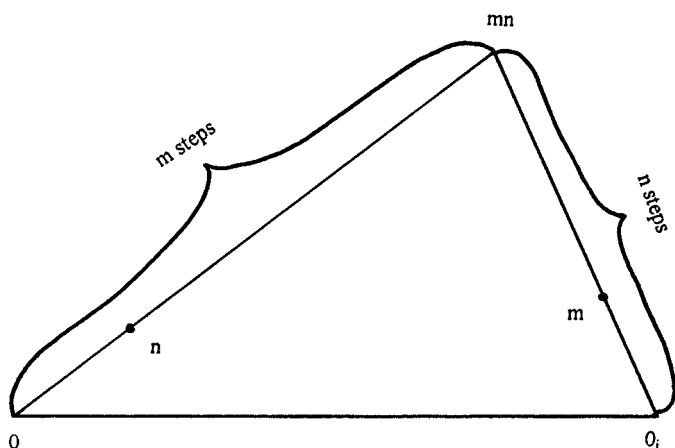


FIG. 3. The opposed parastichy triangle belonging to (m, n) .

Tait sought to use the reverse of a contraction without realizing that a contraction can be reversed in two different ways, as shown in the following definition.

DEFINITION. 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*.

The following three propositions proved in Adler (1), taken together, constitute what has been called the *Fundamental Theorem of Phyllo-taxis* (8).

PROPOSITION 3. If (m, n) is a visible opposed parastichy pair, then there is a unique integer t such that (m, n) is the end result of a finite sequence of extensions starting with the visible opposed parastichy pair $(t, t + 1)$.

PROPOSITION 4. $(t, t + 1)$ is a visible opposed parastichy pair if and only if $1/(t + 1) \leq d \leq 1/t$, where d is the divergence.

PROPOSITION 5. Suppose that $[x/y, u/v]$ is the range of all possible values of d for which the opposed parastichy pair (v, y) is visible. Assume that x/y and u/v are in lowest terms. Let m be the mediant between x/y and u/v , namely $m = (x + u)/(y + v)$. Then the left extension of (v, y) is a visible opposed parastichy pair if and only if d is in the segment $[x/y, m]$, and the right extension of (v, y) is a visible opposed parastichy pair if and only if d is in the segment $[m, u/v]$.

11. AN ALGORITHM FOR CALCULATING THE RANGE OF d

Propositions 3, 4, and 5 provide an algorithm for determining the range of possible values of the divergence for any given visible opposed parastichy pair (m, n) : Starting with (m, n) form successive contractions until you reach one of the form $(t, t + 1)$. Write these now in reverse order to obtain a sequence of extensions starting from $(t, t + 1)$. Write next to each extension L or R, to indicate whether it is a left or right extension of the pair that precedes it. Then use Proposition 5 to obtain the corresponding range of values of d . In the example below we use the algorithm to determine the range of possible values of d for the visible opposed

parastichy pair (34, 21):

Contractions	Extensions	Range of d
(34, 21)	(2, 3)	$[1/3, 1/2]$
(13, 21)	L (5, 3)	$[1/3, 2/5]$
(13, 8)	R (5, 8)	$[3/8, 2/5]$
(5, 8)	L (13, 8)	$[3/8, 5/13]$
(5, 3)	R (13, 21)	$[8/21, 5/13]$
(2, 3)	L (34, 21)	$[8/21, 13/34]$

Note that, contrary to Tait's assertion, each extension narrows the range of possible values of d .

12. THE GEOMETRIC MEANING OF A SIMPLE CONTINUED FRACTION

In Section 11 we saw how to determine the range of possible values of d for any given opposed parastichy pair that is visible. In order to proceed in the opposite direction, that is, to find which opposed parastichy pairs are visible for any given d , it is first necessary to understand the geometric meaning of the continued fraction for d . It is customary to introduce simple continued fractions either via the Euclidean algorithm or via Farey sequences. The geometric meaning of a simple continued fraction is implicit in the Farey sequence approach. It was made explicit for the first time by Adler (2), where it was shown that a simple continued fraction represents a median nest of intervals.

To construct the median nest that defines a particular number n , we proceed as follows: On the positive half of the real line designate 0 as $0/1$, and designate infinity as $1/0$. Insert the median between these two, namely $1/1$. It divides the half-line into two segments, namely $[0/1, 1/1]$ on the left, and $[1/1, 1/0]$ on the right. If n is in the left segment, write 0 as the first bit in a sequence of bits that will represent the nest of intervals that we are constructing to represent n . If n is in the right segment, write 1 as the first bit. Now, in the segment that contains n insert the median between its ends, thus dividing it into two segments, and write down as the second bit 0 or 1, according as n is in the left or right segment. Continue in this way, each time inserting the median between the ends of the segment that contains n , and writing 0 or 1 as the next bit in the sequence, according as n is in the left piece or the right piece of the segment just divided.

It is easily seen that the nested set of smaller and smaller intervals containing n is a genuine nest of intervals, and that n is the only number

in the nest. The sequence of bits we have used to represent the nest therefore also represents the number n . (If n is irrational, there will be only one such non-terminating sequence. If n is rational, there will be two. One of the two contains only a finite number of 1's and continues after the last 1 with all 0's. The other contains only a finite number of 0's and continues after the last 0 with all 1's.) The sequence of bits may be seen as a sequence of clusters of 0's and 1's, as shown in the example below:

$$\begin{array}{ccccccccc} \underbrace{11111}_{a_0} & \underbrace{00}_{a_1} & \underbrace{111}_{a_2} & \underbrace{0000}_{a_3} & \underbrace{1111}_{a_4} & \underbrace{00}_{a_5} & \dots & & \\ & & & & & & & \dots & \end{array}$$

Let a_0 be the number of 1's in the first cluster. $a_0 \geq 0$. Let a_1 be the number of 0's in the second cluster, a_2 the number of 1's in the third cluster, etc. In general, a_i stands for a number of 1's if i is even, and for a number of 0's if i is odd. For $i > 0$ $a_i \geq 1$. Then $a_0 + 1/a_1 + 1/a_2 + 1/a_3 + 1/a_4 + \dots$, (where everything that follows a division sign is understood to be under it), is the simple continued fraction for n . If the sequence a_i is terminating, its last term will be infinity. Leaving out the last term will give the continued fraction as it is usually written. However, the infinity should be retained for our purposes.

13. ONE ROLE OF THE CONTINUED FRACTION FOR d

Now let us assume that $n = d$, the divergence of a leaf distribution, which by definition is $\leq \frac{1}{2}$. Then $a_0 = 0$. If $a_1 = t \geq 1$, the first 0 in that cluster tells us that $d \leq 1$, the second 0 tells us that $d \leq \frac{1}{2}$, the third one tells us that $d \leq \frac{1}{3}, \dots$, and the last 0 in the cluster tells us that $d \leq 1/t$. The first 1 that a_2 stands for tells us that $d \geq 1/(t+1)$, so that $1/(t+1) \leq d \leq 1/t$. Then, from Proposition 4 in Section 10, the opposed parastichy pair $(t, t+1)$ is visible. By Proposition 2, all of its contractions, $(t, 1), (t-1, 1), (t-2, 1) \dots (1, 1)$ are also visible. Now by Proposition 5, by starting with $(t, t+1)$, we get further visible opposed parastichy pairs by taking first $a_2 - 1$ consecutive right extensions, then a_3 left extensions, then a_4 right extensions, etc., each set of a_i extensions for $i > 2$ being left or right according as i is odd or even. Thus we see that *the continued fraction expansion for the divergence d determines which opposed parastichy pairs are visible*. What we have outlined here is not restricted to divergences that actually occur in plants. It is a theorem of pure mathematics that applies to any cylindrical point-lattice generated by points placed at equal intervals on a single genetic spiral.

From the general algorithm developed here, others applicable to special cases have been derived (9).

14. TWO EXAMPLES

To illustrate what was developed in Section 13, we give two examples, one of a divergence that does not occur on any plants, and one that does occur on some. The divergence $d = \sqrt{3}/4$ does not occur on any plant, but can be used nevertheless on a single genetic spiral to generate a point-lattice on a cylinder. The simple continued fraction for this number is

$$0 + 1/2 + \overline{1/3 + 1/4}$$

where the bar indicates that the pair of terms $1/3 + 1/4$ is repeated over and over again ad infinitum. Then, according to Section 13, the visible opposed parastichy pairs associated with this value of the divergence are (2, 3), and the consecutive contractions (2, 1) and (1, 1); then, starting from (2, 3), two right extensions, namely, (2, 5) and (2, 7); then four left extensions, namely, (9, 7), (16, 7), (23, 7) and (30, 7); then three right extensions (30, 37), (30, 67) and (30, 97); then four left extensions (127, 97), (224, 97), (321, 97) and (418, 97); etc., with three right extensions from here on alternating with four left extensions.

The divergence $d = 1/(3 + \tau^{-1})$ does occur on some plants. The simple continued fraction for this number is

$$0 + 1/3 + 1/1 + \overline{1/1}.$$

The visible opposed parastichy pairs associated with this value of the divergence are (3, 4) and the consecutive contractions (3, 1), (2, 1), and (1, 1); then, starting from (3, 4), the extensions that are visible are alternately left and right, namely, (7, 4), (7, 11), (18, 11), (18, 29), etc.

15. A SECOND ROLE OF THE CONTINUED FRACTION FOR d

The opposed parastichy pair on a plant that catches the eye is the conspicuous opposed parastichy pair, defined in Section 9. It is determined by the two leaves that are nearest to leaf 0, one on the right and one on the left. When we try to identify which leaves are capable of qualifying as the leaves nearest leaf 0, we find another way in which the continued fraction for the divergence enters into the picture.

DEFINITION. There is a sequence of points $n_1 = 1, n_2, n_3, \dots, n_i, \dots$ with the property that each n_i with $i > 1$ is the first lattice point with $n_i > n_{i-1}$ that is closer to the line $0L$ than n_{i-1} (Fig. 4). These were called "principal neighbors" by Coxeter (7) and "points of close return" by Adler (1).

The vertical component of the distance between leaf n_i and leaf 0 is m_i , where r is the rise. Since the horizontal component is smaller for this leaf than for any point of close return that precedes it in the sequence, it may become the leaf nearest leaf 0 if r is small enough. Thus d alone does not determine all the properties of a leaf arrangement, contrary to the statement by Braun cited in Section 2. The value of the rise r determines which of the n_i are the two leaves nearest leaf 0, and hence determines the

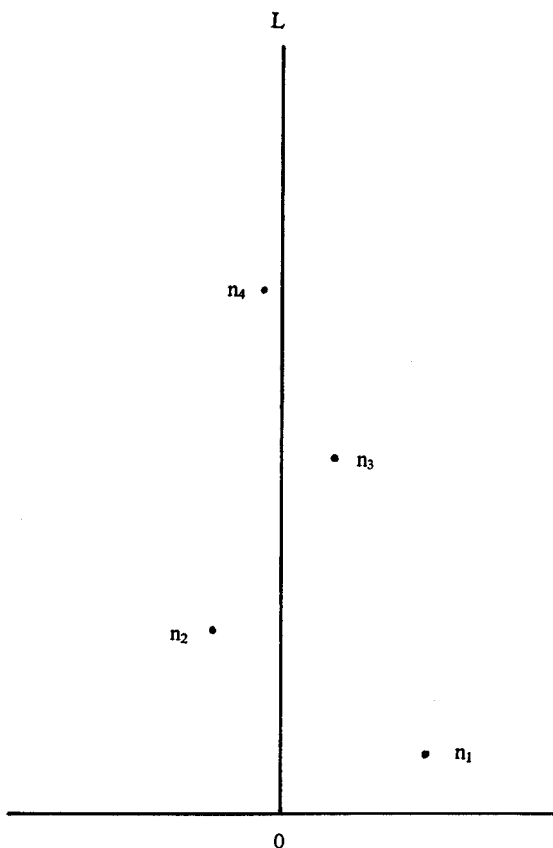


FIG. 4. Points of close return.

conspicuous opposed parastichy pair. Coxeter (7) showed that the n_i are the denominators of the successive principal convergents of the expansion of d as a simple continued fraction.

16. A CAUSAL EXPLANATION

Nearly all observed divergences for a leaf distribution on a single genetic spiral have the form $1/(t + \tau^{-1})$. The continued fraction expansions for all these divergences have the common property that all their terms after the first are equal to 1. The Adler model of phyllotaxis provides a causal explanation of this fact. In the Adler model it is assumed that there is a period in the growth of a stem in which the rise is decreasing and the minimum distance between leaves is maximized. Under these conditions, it can be shown that the two leaves nearest leaf 0 must be equidistant from it, so that they lie on a circle with 0 as center. As r decreases, the next higher point of close return will join them so that there will be three points of close return on a circle with 0 as center (Fig. 5), and then with a further decrease of r it will displace one of them as leaf nearest 0. The three consecutive points of close return that are on the circle in Fig. 5 are the denominators of consecutive principal convergents of d , say, q_{n-1} , q_n , and q_{n+1} , and so are connected by the recurrence relation $q_{n+1} = q_{n-1} + a_{n+1}q_n$, where a_{n+1} is the term of the continued fraction for d that corresponds to the principal convergent p_{n+1}/q_{n+1} . If $a_{n+1} > 1$ there are leaves with leaf numbers greater than q_n that are intermediate neighbors on the segment that joins q_{n-1} and q_{n+1} (7), and that are not closer to $0L$ than q_n . But this is impossible if q_{n-1} , q_n and q_{n+1} are all equidistant from leaf 0. Hence under the assumption of maximization of the minimum distance between leaves, it is necessary that $a_{n+1} = 1$. As r continues to decrease, one term after another of the continued fraction for d is compelled to be equal to 1. While d is under this compulsion it alternately increases and decreases. The details of this process (1, 2) are not relevant to the purpose of this article and so are not given here.

17. PROPOSED FUNCTIONAL EXPLANATIONS

Why does nature have a preference for divergences in which the terms after the first in the continued fraction for d are all equal to 1? It has been proposed that the process that imposes this property on the values of d has been perfected by natural selection because it has survival value for the plant. However, there has been no consensus among botanists on what trait produced by this process has the postulated survival value. Two

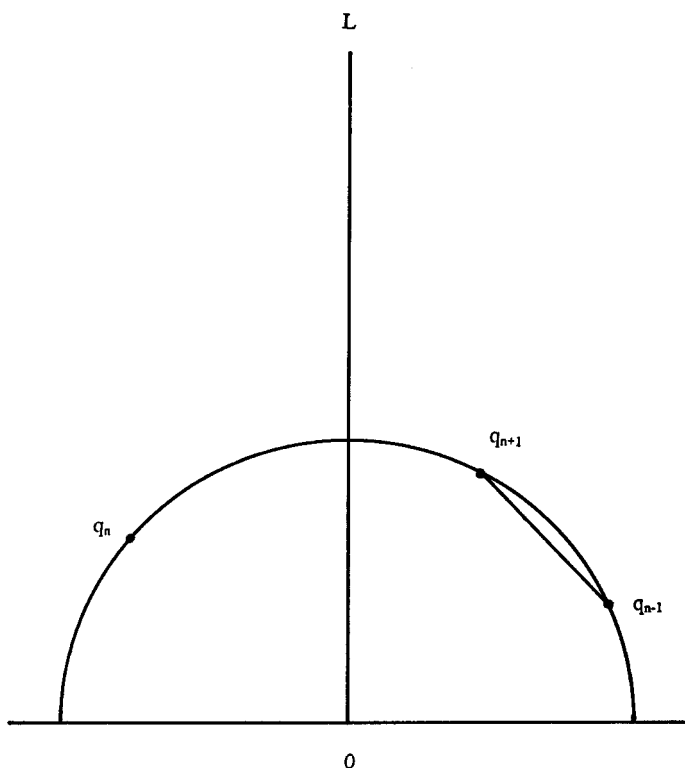


FIG. 5. Three consecutive points of close return that are equidistant from 0.

different theories have been proposed invoking different properties alleged to follow from these values of d . One theory is that these values of d distribute the leaves around a mature stem in such a way as to minimize the shading of lower leaves by those above them, thus maximizing the amount of light they receive. Wiesner (16) claimed to have proved this theory experimentally. However, his experiment merely proved what was known in the first place, that upper leaves partially shade the lower leaves. His data did not show that the so-called "golden angles" shade them the least. Leigh (10) undertook a theoretical proof that this was so, but his argument was not conclusive in that it failed to take into account the influence of the internode distance. The other theory is that the advantage the golden angles give the plant is found at the growing tip of the stem, where the leaf embryos are crowded together, and not on the mature stem, where the leaves are widely separated and the internode distance is elongated. Airy (3) proposed this theory and demonstrated that close

packing of equal spheres around a cylinder does indeed cause the numbers of conspicuous opposed parastichies to be consecutive Fibonacci numbers. In support of his theory he argued that "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."

18. SUMMARY

We have identified three ways in which the continued fraction for the divergence plays a role in phyllotaxis: (1) It determines which opposed parastichy pairs are visible. (2) The points of close return are the denominators of the principal convergents of the continued fraction. (3) When maximization of the minimum distance between leaves is in effect as r decreases, successive terms of the continued fraction are compelled to be equal to 1. It has been proposed in two different theories that this property of the divergence has survival value for a plant, but the arguments in support of these theories are not conclusive.

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