The Fundamental Theorem of Phyllotaxis revisited

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Abstract
(July 2024): This paper has now been superseded and, whilst still mathematically correct, should be considered obsolete.

Jean’s ‘Fundamental Theorem of Phyllotaxis’ (Phyllotaxis: a systematic study in Plant Morphogenesis, CUP 1994) describes the relationship between the count numbers of observed spirals in cylindrical lattices and the horizontal angle between vertically successive spots in the lattice. It is indeed fundamental to observational studies of phyllotactic counts, and especially to the evaluation of hypotheses about the origin of Fibonacci structure within lattices. Unfortunately the textbook version of the theorem is incomplete in that it is incorrect for an important special case. This paper provides a complete statement and proof of the Theorem.

Note
This paper was first uploaded to arXiv in 2012, and the counterexample here to Jean’s theorem as he stated it remains valid. Since that time Infang Publishing has published my book-length treatment of Mathematical Phyllotaxis, ISBN 0993178960. This book puts the (minor) significance of the problem in more context and supersedes this paper, which should be considered obsolete – Jonathan Swinton, July 2024.

1 Introduction
Mathematical phyllotaxis is the study of the patterns that appear in two-dimensional cylindrical lattices, given particular motivation by the striking appearance of high Fibonacci numbers in a range of biological settings such as the spirals on a sunflower [6]. Although static analyses of lattices cannot in themselves explain the appearance of these numbers [12], they are essential both in relating what can actually
be biologically observed to hypothesises about the underlying order, and in forming a basis for dynamical models of lattice formation [8,10,2] that can, it is claimed, explain Fibonacci numbers and related structure in biological form. More specifically, a phyllotactic theory of lattices creates a model for which lines in the lattice are most likely to be remarked on by a human observer. In the case of the sunflower or the fir cone, these lines may be those which join adjacent points in the lattice, which may be defined in different ways as contact parastichies [9,6] or principal parastichies [12]. A slightly more general idea is to identify those pairs of lines that wind in opposite directions as opposed parastichies, or alternatively those lines which can be thought of as characterising the lattice, which were defined as generating parastichies by Turing [12] or equivalently as visible parastichies by Jean [6].

Jean presents the most complete description in the literature of mathematical phyllotaxis in his textbook [6], and deserves considerable credit both for innovation and a substantial work of integration, bringing together a range of biological datasets and historical mathematical approaches. One major contribution is what he calls the Fundamental Theorem of Phyllotaxis which he attributes in a special case to Adler [1]. The basic idea of the theorem is a very useful conceptual one. Cylindrical lattices can be, for these purposes, completely characterised by the angle of rotation between successive points called the divergence. If a lattice is seen to possess a specific pair of generating and opposed parastichies, characterised in a natural way by a pair of integers, then there is a constraint on the allowable values of the divergence. The theorem shows that for any pair of integers not both equal to 1 there are exactly two intervals of nonzero width on which the divergence will create the required generating and opposed parastichies. Unfortunately, however, in the form stated by Jean the Theorem needs modification in a range of special but important cases. The goal of this note is to restate the Theorem completely. First we give the necessary background about two-dimensional cylindrical lattices, and give a characterisation of which divergence values correspond to a given generating pair. After restating the Fundamental Theorem in Jean's formulation and demonstrating a counter example, we then reprove a suitably corrected Theorem.

Unbeknown to Jean and Adler, Turing had also considered very similar problems, but this work was unpublished at his death in 1954 [11]. It remained accessible but obscure in the Turing Archive in King's College Cambridge, until being published in his collected works in 1992 [12], well after the relevant papers of Jean and Adler. As a secondary aim, this paper points out the ways in which Turing anticipated the later, more widely known work.

2 Background

This section contains a number of statements without proof that are fairly obvious on examining a diagram. They can be made rigorous by eg the use of congruences [12].

We consider a cylinder of circumference 1 and extending infinitely in the vertical direction, with an origin and coordinates \((x,z), 0 \leq x \leq 1\). For any \(0 \leq d \leq 1\), we can construct a lattice \(d\) by rotating by an angle \(2\pi d\) around the cylinder from the origin.
and rising by \( z = 1 \), and repeating. This creates the set of points \((x, z) = (d_m, m)\) where \( m \) is any integer and \( d_m = md - \lfloor md \rfloor \) and \( [x] \) is the nearest integer to \( x \), so that \(-\frac{1}{2} \leq d_m \leq \frac{1}{2} \). Since taking \([\frac{1}{2}] = 0\) and \([\frac{1}{2}] = 1\) map to the same point on the cylinder we will allow the function \([x]\) to take the multiple values 0, 1 at the point \( x = \frac{1}{2} \). We call \((d_m, m)\) the point \( \ell_m \), and from now on assume \( m \neq 0 \). The vertical component is called the \textit{rise}.

By construction we have excluded lattices with more than one point at each rise. More generally if there are \( f \) such points spaced equally around the cylinder we would describe the lattice as having \textit{Jugacy} \( f \), but we restrict to \( f = 1 \) here.

A parastichy of order \( m \) is the infinite line through the origin and \( \ell_m \) with slope \( d_m/m \). There are two possible lines on the cylinder through 0 and \( \ell_m \) corresponding to winding in opposite directions and this choice of slope is equivalent to choosing the line that traverses the smallest \( x \) distance between 0 and \( \ell_m \), leaving an ambiguity when \([md] = \frac{1}{2} \). The portion of this line between 0 and \( m \) defines the vector \( \mathbf{m} \), again with an ambiguity when \([md] = \frac{1}{2} \). An \( m \)-parastichy is a member of the family of \( m \) distinct lines containing the origin-parastichy of order \( m \) and the parallel lines to it through the points \( 1, \ldots, m - 1 \). If a point \( \ell_p \) is on an \( m \)-parastichy then so is \( \ell_{p+m} \). See Figure [1].

A pair of (parastichy) numbers \((m, n)\) define a pair of points \( \ell_m, \ell_n \) and vectors \( \mathbf{m}, \mathbf{n} \). \((m, n)\) is \textit{opposed} if \( d_m/m \) and \( d_n/n \) have opposite sign. In the case when \([md] = \frac{1}{2} \) we define the parastichy pair \((m, m)\) as the pair combining each of the choices of direction around the cylinder. There remains an ambiguity when \([md] = \frac{1}{2} \) or \([nd] = \frac{1}{2} \) and \( m \neq n \) which could be resolved by a specific choice of direction although it is not of significance subsequently.

There is a natural relationship between a cylindrical lattice and a corresponding periodic lattice in the plane, and the \( m \)-parastichies also define an infinite family of \( m \)-parastichies in the plane lattice. A pair is \textit{generating} for \( d \) if it generates the lattice in the plane in the sense that every point can be expressed as a vector sum \( u\mathbf{m} + v\mathbf{n} \) for integer \( u, v \). It is necessary, but not sufficient, for a generating pair \((m, n)\) to be coprime for if they have a common factor \( k \) all rises, including 1 must be a multiple of \( k \). This is effectively the definition given by Turing [12], and identical to the \textit{visible} pair defined by Jean [6] in a number of different equivalent ways. Since Jean [6] gives no proof of that equivalence we give it in the Theorem below which also establishes the identity with the Turing definition, and in the process modify some of Jean's definitions for extra precision. I have chosen to stick with Turing's word \textit{generating} over Jean's \textit{visible} for these identical concepts as I think the latter word carries confusing connotations in the identification of parastichy counts.

We make use of the determinant \( \Delta_{mn} \) of a pair \((m, n)\), defined as

\[
\Delta_{mn}(d) = |nd| m - |md| n = (nd - d_n)m - (md - d_m)n = ndm - mnd,
\]

\footnote{Note that the definition is such because any non collinear vectors would generate the lattice \textit{in the cylinder}.}
Figure 1: (4,5) is a generating and opposed pair for the cylindrical $d = 17/72$ lattice. The parallelogram defined by the pair tiles the lattice and every lattice point is at a vertex of one of the parallelograms; the edges of the parallelograms form the parastichy lines. The blue lines highlight the family of 4-parastichies and the red lines the family of 5-parastichies.
except for the special case $\Delta_{mn}(\frac{1}{2}) = m$ (where we have picked $\lfloor \frac{1}{2} \rfloor = 1$ in the $\lfloor nd \rfloor$ and $\lfloor \frac{1}{2} \rfloor = 0$ in the $\lfloor md \rfloor$).

**Theorem 1.** (Compare Theorem 4.2 of Jean [6].) The following are equivalent

1. The pair $(m, n)$ is generating in the lattice $d$.
2. The pair $(m, n)$ has a point of the lattice $d$ at every intersection of the lines of the pair.
3. The points $0, \ell_m, \text{ and } \ell_n$ form a nondegenerate triangle which contains no other point of the lattice $d$ internally.
4. $(m, n)$ satisfy $|\Delta_{mn}(d)| = 1$.

**Proof.** If a pair of vectors are collinear in the plane, they cannot be generating. If they are not collinear, the parallelogram formed by any pair can be used to tile the cylinder. This tiling will contain lattice points exactly at the vertices of each parallelogram iff the pair is generating, because if it has an internal point it must be a nonintegral sum of the pair. This shows $1 \iff 3$. Moreover the tiling produces the parastichy families of order $m$ and $n$, so these must always intersect at a lattice point iff the pair is generating. This shows $1 \iff 2$.

A pair is generating iff it can express the unit vector $(0 \leq d < 1, 1)$ as a sum of $m$ and $n$ in the plane. In plane coordinates, we have

\[
\lfloor nd \rfloor m - \lfloor md \rfloor n = (\lfloor nd \rfloor d_m - \lfloor md \rfloor d_n, \lfloor nd \rfloor m - \lfloor md \rfloor n) = (\lfloor nd \rfloor (md - \lfloor md \rfloor) - \lfloor md \rfloor (nd - \lfloor nd \rfloor), \Delta_{mn}) = \Delta_{mn}(d, 1)
\]

If $\Delta_{mn} = 1$ we are done, and if $\Delta_{mn} = -1$ we take the combination $\lfloor md \rfloor n - \lfloor nd \rfloor m$ of opposite sign, so if $|\Delta_{mn}| = 1$ then $(m, n)$ is generating. This shows $4 \iff 1$.

To prove $1 \iff 4$, the central idea (of Jean and Adler and Turing) is to continue the $m$ and $n$ parastichies away from the origin until they cross again, so first we have to dispose of the case when the two parastichies are parallel. If $m$ and $n$ are parallel, then they are not generating, and moreover $d_m/m = d_n/n$ so $\Delta_{mn} = 0$ and conversely. If they are not parallel then in the plane the parastichy of order $m$ through $(0, 0)$ and $(d_m, m)$ and the parastichy of order $n$ through $(1, 0)$ and $(d_n, n)$ must meet at the point

\[
\left(\frac{md_n}{\Delta_{mn}}, \frac{nd_m}{\Delta_{mn}} - 1, \frac{mn}{\Delta_{mn}}\right).
\]

If $(m, n)$ is generating this must be a point of the lattice and so have rise equal to both $km$ and $k'n$ for integer $k, k'$, so $n = k\Delta_{mn}$ and $m = k'\Delta_{mn}$. But since $m$ and $n$ are coprime, $|\Delta_{mn}| = 1$.

There are close connections with the theory of Farey sequences, as mentioned in Jean [6] and in more detail in Jean [5], which can be exploited to give different versions of this proof, but we do not pursue that here.
The existence of two choices for \( \Delta \) is a reflection of the symmetry arising from the choice of direction around the cylinder which corresponds to \((m, n, d, \Delta) \rightarrow (m, n, 1-d, -\Delta)\) and \((m, n, d, \Delta) \rightarrow (n, m, d, -\Delta)\), so it is possible to force at least one of \(m \leq n\) or \(|d| < \frac{1}{2}\) or \(\Delta = +1\) if we wish. Indeed Jean chooses to focus in the case \(d < \frac{1}{2}\), but here we allow either choice but recognise that the resulting intervals for \(d\) are related by this symmetry.

Figure 1 shows a generating opposed pair, and Figure 2 shows a variety of pairs which are not.

The Fundamental Theorem gives conditions for \(d\) if \((m, n)\) are generating and opposed. We will prove it by first finding conditions for \((m, n)\) to be generating.

3 Finding \(d\) given \((m, n)\) generating

The previous Theorem gives only an implicit form for \(d\). Here we find the explicit intervals for \(d\) on which \(|\Delta_{mn(d)}| = 1\). Given \(m, n\) coprime and \(\Delta = \pm 1\) we want to find those \(d\) such that \(\Delta_{mn}(d) = \Delta\).

If \(m = n\) but \(m \neq n\) we must have \(d = \frac{1}{2}\) and we are done, with \(m = n = 1\), \(\Delta = 1\).

Otherwise, assume for now that \(m < n\). Now take \(u, v\) by solving \(mv - nu = \Delta\), specified uniquely for \(m > 1\) by \(0 \leq u < m\), \(0 \leq v < n\), or for \(m = 1\) by \((u, v) = (0, 1)\) when \(\Delta = 1\) or \((u, v) = (1, n-1)\) when \(\Delta = -1\).

To force \(|md| = u\) and \(|nd| = v\) we need

\[
L_m = \frac{u - \frac{1}{2}}{m} \leq d \leq \frac{u + \frac{1}{2}}{m} = R_m
\]

\[
L_n = \frac{v - \frac{1}{2}}{n} \leq d \leq \frac{v + \frac{1}{2}}{n} = R_n
\]

respectively and \(d\) is in the intersection of the intervals \((L_m, R_m), (L_n, R_n)\). Note that \(\text{eg } (L_n, R_n)\) is centred at \(v/n\) and has width \(1/n\). Then

\[
\begin{align*}
mn(L_n - L_m) &= \Delta + \frac{1}{2}(n - m) \\
mn(R_n - R_m) &= \Delta - \frac{1}{2}(n - m) \\
mn(R_n - L_m) &= \Delta + \frac{1}{2}(m + n) \\
mn(R_m - L_n) &= -\Delta + \frac{1}{2}(m + n)
\end{align*}
\]

So \(L_n > L_m \iff n > m - 2\Delta\), which is always true unless \(\Delta = -1\) and \(n = m + 1\).

Similarly \(R_m > R_n\) if \(n > 2\Delta + m\) which is true unless \(\Delta = 1\) and \(n = m + 1\). So apart from those two cases we have \(L_m < L_n < R_n < R_m\) and the interval \((L_n, R_n)\) is the one we want. To pay attention to the special cases we see that for \(n = m + 1\)

\[
\begin{align*}
\text{sign}(L_n - L_m) &= \text{sign}(\Delta + \frac{1}{2}) = \Delta \\
\text{sign}(R_n - R_m) &= \text{sign}(\Delta - \frac{1}{2}) = \Delta \\
\text{sign}(R_n - L_m) &= \text{sign}(\Delta + n + \frac{1}{2}) = +1 \\
\text{sign}(R_m - L_n) &= \text{sign}(\Delta + n - \frac{1}{2}) = +1
\end{align*}
\]
(a) (5,9) is a generating but not opposed pair.

(b) (9,19) is a nonopposed nongenerating pair which is not collinear.

(c) (5,7) is an opposed but not generating pair.

(d) (1,2) is a nonopposed nongenerating pair which is collinear.

Figure 2: Different types of parastichy pair in the lattice with divergence $d = 17/72$. 
so if \( \Delta = 1 \) we have \( L_m < L_n < R_m < R_n \) while if \( \Delta = -1 \) it is \( L_n < L_m < R_n < R_m \).

We originally assumed \( m < n \). If instead \( m > n \), we can swap \( m \) and \( n \) which will change the sign of \( \Delta \), so we can summarise in

**Theorem 2.** \((m, n)\) is a generating pair in the lattice \( d \) iff \( d \) is in the intervals specified in Table 1.

Armed with Theorem 2, we can now add the additional condition that the parastichy pair be opposed in order to find the Fundamental Theorem.

## 4 The Fundamental Theorem of Phyllotaxis

### 4.1 The Jean formulation

Jean's version [5, 6] of the FTP states

Let \((m, n)\) be a parastichy pair, where \( m \) and \( n \) are relatively prime, in a system with divergence angle \( d \). The following properties are equivalent:

1. There exist unique integers \( 0 \leq u < m \) and \( 0 \leq v < n \) such that \(|mv - nu| = 1 \) and \( d < \frac{1}{2} \) is in the closed interval whose end points are \( u/m \) and \( v/n \);

2. The parastichy pair \((m, n)\) is visible and opposed

### 4.2 Counterexample

Consider the lattice with \( d = 1/12 \). Then the parastichy pair \((1, 3)\) is neither generating nor opposed, so (2) is false. However the unique integers satisfying \(|mv - nu| = 1 \) and \( 0 \leq u < 1 \) and \( 0 \leq v < 3 \) are \( u = 0 \) and \( v = 1 \), and \( d = 1/12 < \frac{1}{2} \) is in the interval \([0/1, 1/3]\), so (1) is true. See Figure 3.

In fact the counterexample holds for all pairs of the form \((1, n)\), and in fairness to Jean it might be argued that 1 and \( n \) might not considered to be coprime, in which case the Theorem still holds, but this interpretation is ruled out by the comment in Appendix 4.1 that non coprime pairs are those that do not produce 'one genetic spiral'. A more powerful defense of the utility of the Jean version of the Theorem is that it is intended for pattern recognition, typically on specimens with large, usually Fibonacci, parastichy numbers in which it is only exceptionally the case that \( m = 1 \). But even discounting the difficulty this error in the special case can cause the reader
Figure 3: (1,3) are not a generating or an opposed pair for the lattice $d = 1/12$. 
in following the argument, it turns out that all modern discussions of the appearance of Fibonacci structure \[8, 7, 3\] invoke a successive sequence of bifurcations from more simple starting conditions, specifically \((1, 1)\) and \((1, 2)\), so it is important to account properly for this case.

5 Opposed generating pairs

We now need to reprove the FTP, which we do by considering on which portion of the \(d\) interval where \((m, n)\) is generating it is also opposing. First we assume \(\Delta > 0\).

\(d_m\) passes through 0 at \(L_m, u/m, \text{and} \ R_m\) and nowhere else in the interval \((L_m, R_m)\), where \(u\) is defined in the proof of Theorem 2. For \(m > 2\), by Theorem 2 the generating interval is \((L_n, R_n)\) and we saw \(L_m < L_n < u/m < v/n < R_n < R_m\), and so within the generating interval \(d_m\) is negative only for \(d < u/m\) and \(d_n\) is negative only for \(d < v/n\). Thus the only region of the generating interval on which \((m, n)\) is opposed is \(u/m < d < v/n\). Under the symmetry, we see the analogous case for \(\Delta = -1\).

The point of this paper, though, is to define the necessary interval when \(m = 1\). For \(n = 1\) we have already seen we must take \(d = \frac{1}{2}\). Otherwise Theorem 2 shows the generating interval (for \(\Delta = +1\)) is of the form \((1/4, 1/2)\) for \(n = 2\) and \(1/n \pm 1/2n\) for \(n > 2\). Since \(d_n\) changes sign every \(1/2n\), in either case, the generating and opposed interval for \(d\) is \((1/2n, 1/n)\). So we can summarise in

**Theorem 3.** *(The Fundamental Theorem of Phyllotaxis).* The following are equivalent

1. \((m \leq n, n)\) is generating and opposed in the lattice \(d\), with \(\Delta_{mn}(d) = \Delta\)

2.  
   (a) \(m = 1, n = 1, \ d = \frac{1}{2}, \text{and} \ \Delta = 1, \text{or}\)
   
   (b) \(m = 1, n > 1, \ \Delta = +1, \ d \in (1/2n, 1/n), \text{or}\)
   
   (c) \(m = 1, n > 1, \ \Delta = -1, \ d \in 1 - (1/2n, 1/n), \text{or}\)
   
   (d) \(1 < m < n, \ d \in (u/m, v/n), \ \Delta = \pm 1, \text{where} \ u, v \text{are the unique integers} \ 0 \leq v < n, \text{and} \ 0 \leq u < m \text{such that} \ mv - nu = \Delta.\)

Part of the significance of this theorem, as Adler [1] and Turing [12] showed, is that if \(m = F_k\) and \(n = F_{k+1}\) are successive members of the Fibonacci sequence, then the interval for \(d\) is \((F_k - 2/F_k, F_k - 1/F_k)\) which rapidly converges to the point \(d = \tau^{-2}\) where \(\tau\) is the golden ratio.

6 Discussion

This correction to the Fundamental Theorem of Phyllotaxis does not reduce its centrality in the relationship between observed parastichy counts and the underlying mathematical structure of cylindrical lattices. Nor does recasting it partly in the earlier work of Turing remove the justifiable priority claims of Jean and Adler in its development, since that earlier work was languishing unpublished and incomplete in
the Turing archive when they independently published theirs. Nevertheless, this paper has taken advantage of the correction needed to the special case when one of the parastichy numbers is 1 in order to put the Theorem in a more accurate historical context and point out the common ideas of these authors.

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