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Emergence of the Golden Angle in Flower Heads

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Emergence of the Golden Angle in Flower Heads

Przemyslaw Prusinkiewicz

Abstract. Phyllotaxis—the arrangement of plant organs around their supporting axes —is an important attribute of plant architecture. Recent experimental data show that the first phase of typical phyllotactic pattern development in flower heads can be abstracted as an extension of the Fibonacci substitution L → LS, S → L. We demonstrate that the most intriguing geometric feature of phyllotaxis, the golden angle between the emerging organs, is a mathematical consequence of this substitution process.

1. INTRODUCTION. Plants have been a source of enjoyment for millennia. The harmony of plant forms and patterns inspires poets and artists, underlies the beauty of gardens and landscapes, and has attracted the multidisciplinary interest of scientists for centuries. Among the many aspects of plant form conducive to in-depth analysis, one holds a preeminent place due to its geometric character and particularly intriguing mathematical properties. It is the arrangement of plant organs into regular, geometric patterns, called *spiral phyllotaxis*.

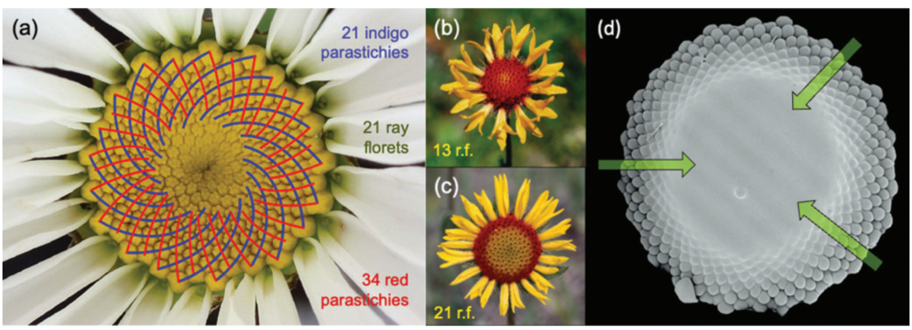

Figure 1. Phyllotactic patterns in heads. (a) A sample daisy head, with 21 and 34 parastichies winding in opposite directions, and 21 petal-like ray florets. b, c) Additional examples: gaillardia heads, with 21 and 13 ray florets. (d) A scanning electron photograph of a developing gerbera head, showing progression of patterning from the head rim toward the center. Microscopy image courtesy of Teng Zhang and Paula Elomaa, adapted from [1].

The typical[1] arrangement of *florets* (individual flowers) in the heads of sunflower and other plants in the Aster family is the iconic example of spiral phyllotaxis (Figure 1a). Its analysis reveals two intriguing geometric features. First, adjacent organs filling the head are arranged into two sets of conspicuous spirals—called parastichies—winding in opposite directions. The numbers of *parastichies* in these sets are consecutive Fibonacci numbers. Second, the number of *ray florets* with enlarged

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[1]Other arrangements also occur in nature, but are less frequent [2, 3] and are not considered here.

petals on the pattern periphery is also a Fibonacci number (see also Figure 1b,c). Recall that Fibonacci numbers are defined by recursion $f_0 = 0$, $f_1 = 1$, $f_{n+1} = f_n + f_{n-1}$ for $n \geq 1$ [4, 5]; as we will deal with them throughout the paper, it is convenient to write down the first few numbers:

n	0	1	2	3	4	5	6	7	8	9	10
f_n	0	1	1	2	3	5	8	13	21	35	55

A causal explanation of the development of phyllotactic patterns resulting in their geometric properties has long attracted broad interdisciplinary interest [2, 6, 7]. The cornerstone hypothesis, formulated by Wilhelm Hofmeister [8] and amended by Mary and Robert Snow [9, 10], states that a new organ (an organ *primordium*) is initiated where and when sufficient space emerges for it during plant development. How can Fibonacci numbers of organs on the rim and parastichies arise in this process? Somewhat counterintuitively, given the commonality of spiral phyllotaxis across the plant kingdom, the answer to this question is species-dependent [11]. For heads, it was found only recently by Teng Zhang et al. [1] through a combination of experimental data, mathematical reasoning, and computational modeling.

In most heads, phyllotactic patterning progresses centripetally, from outside in (Figure 1d). The central region is initially empty, limiting interactions between primordia to their immediate neighbors. The first phase of patterning, taking place on the rim of the growing head, is an essentially one-dimensional process that can be abstracted as the placement of points on a circle (Figure 2). As the head grows and the rim expands, the arc-length distances between primordia increase, periodically creating gaps large enough for new primordia to emerge. If, during the expansion, each primordium remained equidistant from its neighbors (intuitively the simplest dynamic), the gaps on both of its sides would increase equally. In the context of Hofmeister's hypothesis, this dynamic would result in a geometric progression of primordia numbers in discrete steps: 1, 2, 4, 8, etc. Unexpectedly, Zhang et al. [1] observed that, as the rim expands, incipient primordia are displaced toward their older neighbor, resulting in a shorter gap than the one toward the younger neighbor. This asymmetry delays the insertion of the next generation of primordia into the shorter gaps by approximately one step, compared to insertion into the longer gaps. The delay leads to a progression of gap and primordia numbers on the head rim following the

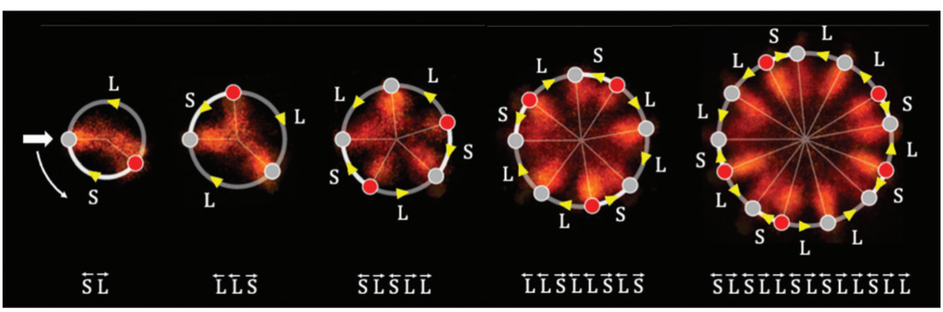

Figure 2. Early patterning of organ primordia in a growing gerbera flower head. Red smudges visualize a molecular marker of the plant hormone auxin, which determines positions of the incipient primordia. Small circles represent primordia positions abstracted as points, with the newly inserted primordia highlighted in red. Symbols L and S indicate long and short gaps between primordia, respectively. Arrows indicate gap polarity, pointing from the younger to the older primordium. Note that, when a new primordium is inserted, the short gap always forms on the side of the older neighbor, and this orientation alternates between clockwise and counterclockwise in consecutive steps. The gap sequence shown beneath each image is obtained by scanning the pattern of gaps counterclockwise, beginning at the first primordium, as indicated by the larger arrows. Microscopy images courtesy of Teng Zhang and Paula Elomaa, adapted from [1].

Fibonacci sequence (Figure 2). The pattern on the head rim then serves as a template organizing subsequently generated primordia into a two-dimensional arrangement resembling a lattice, within which parastichies arise.

In many plants, new primordia are inserted sequentially near the center of the supporting surface, and the pattern expands centrifugally [12] (Figure 3a). An important attribute of this process is the angle between consecutively inserted primordia, known as the *divergence angle* (Figure 3b). Intriguingly, this angle often approximates the *golden angle*, obtained by dividing the full angle according to the golden ratio (Figure 3c) [7, 13]. In flower heads, however, the divergence angle is difficult to define because primordia on the rim are inserted in bursts rather than sequentially, and the golden angle is not evident. Is it present at all?

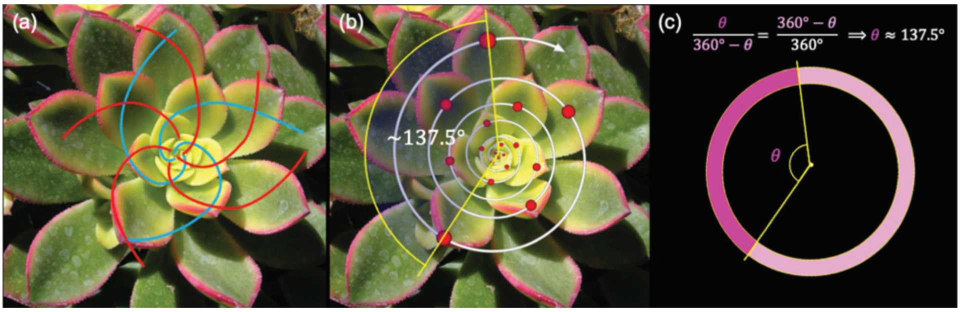

Figure 3. Phyllotaxis in *Semprevivum*. (a) The parastichy pattern. (b) The sequence of organ initiation, indicated by a spiral. The observed divergence angle is close to 137.5°. (c) A mathematical definition of the golden angle θ.

Here we show that it is possible to assign indices to the primordia arising on the rim—i.e., in the first, one-dimensional phase of patterning—so that the divergence angle between all pairs of consecutively numbered primordia approximates (or, under specific conditions, equals) the golden angle. Moreover, this assignment is persistent, i.e., primordia created earlier keep their indices as new primordia are added. A formal statement of this claim and its proof are based on a detailed analysis of the pattern of gaps that develops on the head rim through bursts of primordia insertion. We begin by devising a mathematical model of this development.

2. A MODEL OF THE PATTERN OF GAPS. We express our model using the formalism of *L-systems*: a mathematical framework for simulating and analyzing plant development originated in 1968 by Aristid Lindenmayer [14]. A tutorial introduction to L-systems with extensions used in this paper can be found in [15].

An L-system is defined by three components: an *alphabet* (a set of *letters*) on which the L-system operates, a set of *rewriting rules* or *productions* that replace these letters with *words* (strings of letters) over the same alphabet, and an *axiom* or *initial word* from which rewriting begins. An L-system generates *developmental sequences* of words iteratively, in discrete *derivation steps* representing the progress of time by finite intervals. In each step, every letter in the *predecessor word* is replaced by this letter's *successor* specified by the applicable production.

A simple example is the L-system with alphabet {L, S}, axiom S, and productions

$$\mathrm{L} \to \mathrm{LS}, \quad \mathrm{S} \to \mathrm{L}, \tag{1}$$

also known as the *Fibonacci substitution* [16, 17]. The sequence of words w_i it produces begins with $w_1 = \mathrm{S}$, $w_2 = \mathrm{L}$, $w_3 = \mathrm{LS}$, $w_4 = \mathrm{LSL}$, $w_5 = \mathrm{LSLLS}$, $w_6 = \mathrm{LSLLSLSL}$.

Remark 1. It is easy to notice (and prove by induction) that words produced by the Fibonacci substitution satisfy the following criteria: (i) the number f_n of letters in word w_n (length of word w_n) is the n-th element of the Fibonacci sequence; (ii) this word has exactly f_{n-2} letters S and f_{n-1} letters L for $n \geq 2$; and (iii) letters S always occur in isolation.

The Fibonacci substitution captures some elements of primordia patterning on the rim of flower heads. If we interpret letters L and S as long and short gaps between primordia, production S $\to$ L can be viewed as representing growth of a short gap into a long gap, whereas production L $\to$ LS can be viewed as representing the asymmetric division of a long gap into a long and a short gap following the insertion of a new primordium (which is not represented explicitly). The model accounts for the overall increase in the number of gaps (and thus primordia between them) according to the Fibonacci sequence, as well as the numbers of long and short gaps, as observed in real plants (Figure 2). However, the order of gaps is incorrect: the gaps resulting from the insertion of a new primordium always appear in the same order, long (L) followed by short (S), whereas in nature this order alternates between successive steps (Figure 2).

Zhang et al. [**1**] showed that the observed pattern of gaps can be captured by extending the Fibonacci substitution with the notion of gap polarity: an attribute of gaps that controls their subdivision. Representing polarities as arrows above gap symbols, the resulting *polarized Fibonacci substitution* is defined by an L-system with a four-letter alphabet $\overleftarrow{\mathrm{L}}$, $\overrightarrow{\mathrm{L}}$, $\overleftarrow{\mathrm{S}}$, $\overrightarrow{\mathrm{S}}$, axiom $\overleftarrow{\mathrm{S}}$, and productions

$$\overleftarrow{\mathrm{L}} \to \overleftarrow{\mathrm{S}}\,\overrightarrow{\mathrm{L}},\;\; \overrightarrow{\mathrm{L}} \to \overleftarrow{\mathrm{L}}\,\overrightarrow{\mathrm{S}},\;\; \overleftarrow{\mathrm{S}} \to \overleftarrow{\mathrm{L}},\;\; \overrightarrow{\mathrm{S}} \to \overrightarrow{\mathrm{L}}. \tag{2}$$

The developmental sequence it produces begins with

$$\overleftarrow{\mathrm{S}} \Rightarrow \overleftarrow{\mathrm{L}} \Rightarrow \overleftarrow{\mathrm{S}}\,\overrightarrow{\mathrm{L}} \Rightarrow \overleftarrow{\mathrm{L}}\,\overleftarrow{\mathrm{L}}\,\overrightarrow{\mathrm{S}} \Rightarrow \overleftarrow{\mathrm{S}}\,\overrightarrow{\mathrm{L}}\,\overleftarrow{\mathrm{S}}\,\overrightarrow{\mathrm{L}}\,\overrightarrow{\mathrm{L}} \Rightarrow \overleftarrow{\mathrm{L}}\,\overleftarrow{\mathrm{L}}\,\overrightarrow{\mathrm{S}}\,\overleftarrow{\mathrm{L}}\,\overleftarrow{\mathrm{L}}\,\overrightarrow{\mathrm{S}}\,\overleftarrow{\mathrm{L}}\,\overrightarrow{\mathrm{S}} \cdots,$$

where the yield symbol $\Rightarrow$ indicates the result of a single derivation step. This is the same sequence as displayed in Figure 2.

Remark 2. The polarized Fibonacci substitution retains properties (i) and (ii) of the original Fibonacci substitution (1) listed in Remark 1, as they do not depend on the order of letters S and L; moreover, it also retains property (iii). In addition, productions (2) imply that (iv) gaps S and L have opposite polarities in every word w_n, $n \geq 3$; and (v) these polarities alternate between consecutive words.

3. THE PRIMORDIA INDEXING SCHEME. In the quest for the golden angle, we need to represent primordia explicitly. To this end, we extend the polarized Fibonacci substitution (2) with an additional symbol P, representing a primordium and referred to as a point. The L-system below also introduces a scheme for indexing primordia, which is crucial to the formulation and proof of the main results.

$$\begin{array}{rlclcl|lcl} \text{axiom :} & \mathrm{P_1}\,\overleftarrow{\mathrm{S}}\,\mathrm{P_1} & & & & & & & \\ \text{productions :} & \mathrm{P_i} < & \overleftarrow{\mathrm{L}} & \to & \overleftarrow{\mathrm{S}}\,\mathrm{P_{i+f_n}}\,\overrightarrow{\mathrm{L}} & & \overrightarrow{\mathrm{L}} > \mathrm{P_i} & \to & \overleftarrow{\mathrm{L}}\,\mathrm{P_{i+f_n}}\,\overrightarrow{\mathrm{S}} \\ & & \overrightarrow{\mathrm{S}} & \to & \overrightarrow{\mathrm{L}} & & \overleftarrow{\mathrm{S}} & \to & \overleftarrow{\mathrm{L}} \end{array} \tag{3}$$

The notation $\mathrm{P_i} < \overleftarrow{\mathrm{L}}$ (or $\overrightarrow{\mathrm{L}} > \mathrm{P_i}$) indicates that primordium $\mathrm{P_i}$ is the left (or right) *context* of polarized gap $\overleftarrow{\mathrm{L}}$ (or $\overrightarrow{\mathrm{L}}$). By definition, a production does not affect its

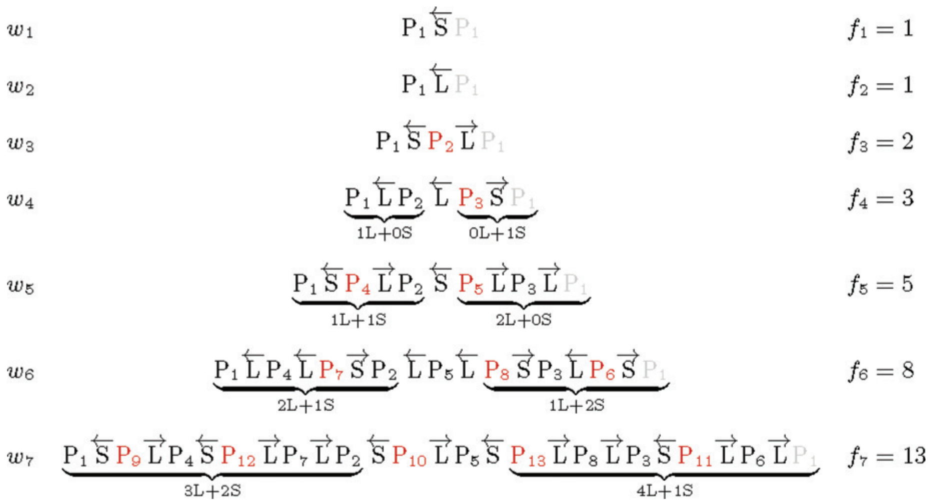

Figure 4. The first seven words generated by L-system (3). Primordia introduced in the current derivation step are highlighted in red. The right column lists Fibonacci numbers f_n that are added to indices of primordia $\mathrm{P_i}$ in word w_n to obtain indices of new primordia $\mathrm{P_{i+f_n}}$ in word w_{n+1}. For example, the index of primordium P_{10} in word w_7 results from adding $f_6 = 8$ to the index of primordium P_2 in word w_6. Left underbraces indicate the counts of gaps L and S between two representative primordia indexed consecutively, in this case P_1 and P_2. Note that these counts are the same for any pair of consecutively indexed primordia within the same word and correspond to consecutive Fibonacci numbers. Right underbraces indicate the gap count between the last and first primordia, $\mathrm{P_{f_n}}$ and P_1. The counts of gaps L and S differ from those between consecutively indexed primordia by ± 1. Theorem 4, which generalizes and proves these observations, is the cornerstone result of this paper.

context, but the context may provide information affecting the result of the production application (the production successor) [15]. In the case of L-system (3), this information is index i of the primordium that delimits the rewritten gap $\overleftarrow{\mathrm{L}}$ on the left or gap $\overrightarrow{\mathrm{L}}$ on the right. It affects the index assigned to the new primordium, calculated as $i + f_n$. The parameter f_n is the nth Fibonacci number, where n is the position of the predecessor word in the developmental sequence (n is thus equal to 1 for the axiom, 2 for the word directly derived from the axiom, etc.).

Accounting for the circular topology of the rim, we assume that L-system (3) operates on *circular words*, i.e., words in which the first and last letters are considered neighbors.[2] This means, in particular, that the primordium denoted by the first letter of each word is not only to the left of the first gap, but also to the right of the last gap. To highlight this relation, circularity is indicated by repeating the greyed-out primordium symbol P_1 at the end of the axiom and each word in Figure 4, which illustrates the operation of L-system (3).

As there are no productions changing primordia indices, their values, assigned at the time of primordium creation, obviously persist. A less obvious property is the subject of the following lemma.

Lemma 3. *For any word w_n, $n \geq 3$, generated by L-system (3), points P_i have unique indices from 1 to f_n and appear in the following subwords:*

[2] Technically, all L-systems considered in this paper operate on circular words; however, the assumption of circularity only affects derivations in the context-sensitive case [18,19].

Number of points	*Index range*	*Subword even n*	*odd n*
f_{n-1}	$1, \ldots, f_{n-1}$	$\mathrm{P_i}\,\overleftarrow{\mathrm{L}}$	$\overrightarrow{\mathrm{L}}\,\mathrm{P_i}$
f_{n-2}	$1 + f_{n-1}, \ldots, f_n$	$\mathrm{P_i}\,\overrightarrow{\mathrm{S}}$	$\overleftarrow{\mathrm{S}}\,\mathrm{P_i}$

Proof. By induction on n.
1. Base step. By examining words w_3 and w_4 in Figure 4 we observe that the lemma holds for $n = 3$ and $n = 4$. Specifically, for $n = 3$ we have $f_{n-1} = f_{n-2} = 1$, and points P_i appear in context $\overrightarrow{\mathrm{L}}\,\mathrm{P_1}$ and $\overleftarrow{\mathrm{S}}\,\mathrm{P_2}$. For $n = 4$ we have $f_{n-1} = 2$ and $f_{n-2} = 1$, and points P_i appear in contexts: $\mathrm{P_1}\,\overleftarrow{\mathrm{L}}$, $\mathrm{P_2}\,\overleftarrow{\mathrm{L}}$ and $\mathrm{P_3}\,\overrightarrow{\mathrm{S}}$.

2. Induction step. Analyzing L-system (3) we observe that the two-letter subwords specified by the Lemma yield the following subwords in a single derivation step:

case	*even n*	*odd n*
1	$\mathrm{P_i}\,\overleftarrow{\mathrm{L}} \Rightarrow \overrightarrow{\mathrm{L}} \triangleleft \mathrm{P_i}\,\overleftarrow{\mathrm{S}}\,\mathrm{P_{i+f_n}}\,\overrightarrow{\mathrm{L}}$	$\overrightarrow{\mathrm{L}}\,\mathrm{P_i} \Rightarrow \overleftarrow{\mathrm{L}}\,\mathrm{P_{i+f_n}}\,\overrightarrow{\mathrm{S}}\,\mathrm{P_i} \triangleright \overleftarrow{\mathrm{L}}$
2	$\overleftarrow{\mathrm{L}} \triangleleft \mathrm{P_i}\,\overrightarrow{\mathrm{S}} \Rightarrow \overrightarrow{\mathrm{L}} \triangleleft \mathrm{P_i}\,\overrightarrow{\mathrm{L}}$	$\overleftarrow{\mathrm{S}}\,\mathrm{P_i} \triangleright \overrightarrow{\mathrm{L}} \Rightarrow \overleftarrow{\mathrm{L}}\,\mathrm{P_i} \triangleright \overleftarrow{\mathrm{L}}$

As in Figure 4, newly inserted points are shown in red. Symbols $\overleftarrow{\mathrm{L}}$ and $\overrightarrow{\mathrm{L}}$, separated by triangles $\triangleleft$ and $\triangleright$, are letters that play no role in the derivations themselves, but whose presence can be inferred from Remarks 1(iii) and 2(iv,v). Specifically, in case 1 for an even n, the subword $\mathrm{P_i}\,\overleftarrow{\mathrm{S}}\,\mathrm{P_{i+f_n}}\,\overrightarrow{\mathrm{L}}$ derived from $\mathrm{P_i}\,\overleftarrow{\mathrm{L}}$ must be preceded by $\overrightarrow{\mathrm{L}}$ because, in every word generated by the polarized Fibonacci substitution, letters S always occur in isolation and have opposite polarity to letters L. For the same reason, in case 2 for an even n, the subword $\mathrm{P_i}\,\overrightarrow{\mathrm{S}}$ must be preceded by $\overleftarrow{\mathrm{L}}$; that, in turn, implies that the successor word $\mathrm{P_i}\,\overrightarrow{\mathrm{L}}$ must be preceded by $\overrightarrow{\mathrm{L}}$ resulting from the production $\overleftarrow{\mathrm{L}} \to \overleftarrow{\mathrm{S}}\,\overrightarrow{\mathrm{L}}$. Analogous reasoning applies to the derivations for an odd n.

With that in mind, consider word w_n for an even $n \geq 4$. From the inductive assumption it follows that word w_n includes f_{n-1} occurrences of subword $\mathrm{P_i}\,\overleftarrow{\mathrm{L}}$, with indices $i = 1, \ldots, f_{n-1}$. In word w_{n+1}, the same points $\mathrm{P_i}$ will thus occur in subwords $\overrightarrow{\mathrm{L}}\,\mathrm{P_i}$ (case 1 for an even n). The subwords derived from $\mathrm{P_i}\,\overrightarrow{\mathrm{S}}$ will result in an additional f_{n-2} points $\mathrm{P_i}$ occurring in subwords $\overrightarrow{\mathrm{L}}\,\mathrm{P_i}$ (case 2), with indices i ranging from $1 + f_{n-1}$ to f_n. This brings the total number of occurrences of subword $\overrightarrow{\mathrm{L}}\,\mathrm{P_i}$ in w_{n+1} to $f_{n-1} + f_{n-2} = f_n$, with indices $i = 1, \ldots, f_n$. In addition, the subwords derived from $\mathrm{P_i}\,\overleftarrow{\mathrm{L}}$ include f_{n-1} new points $\mathrm{P_{i+f_n}}$ (case 1 again), yielding f_{n-1} subwords $\overleftarrow{\mathrm{S}}\,\mathrm{P_i}$ with indices i ranging from $1 + f_n$ to $f_{n-1} + f_n = f_{n+1}$. This concludes the inductive step for an even n. For an odd n the inductive step is analogous. ■

4. SUBWORDS BETWEEN PRIMORDIA. The main theorem of this paper, from which the approximately golden divergence angle follows, characterizes subwords delimited by consecutively indexed primordia, and by the last and first primordia. We use the notation $\mathrm{P_i} u \mathrm{P_j} \prec w$ to indicate that the word $\mathrm{P_i} u \mathrm{P_j}$, consisting of points $\mathrm{P_i}$, $\mathrm{P_j}$ with a subword u between them, is a subword of word w.

Theorem 4 (Fibonacci subword theorem). *In any word $w_n, n \geq 4$, generated by L-system (3):*

1. *every subword $\mathrm{P_i} u \mathrm{P_{i+1}} \prec w_n$ has f_{n-3} letters* L *and f_{n-4} letters* S*;*
2. *subword $\mathrm{P_{f_n}} u \mathrm{P_1}$ has:*

$$\left.\begin{array}{ll} f_{n-3}-1 & \textit{letters } \mathrm{L} \\ f_{n-4}+1 & \textit{letters } \mathrm{S} \end{array}\right\} \textit{for even } n \qquad \left.\begin{array}{ll} f_{n-3}+1 & \textit{letters } \mathrm{L} \\ f_{n-4}-1 & \textit{letters } \mathrm{S} \end{array}\right\} \textit{for odd } n\,.$$

Proof. By induction on n.

1. Base case. Figure 4 shows gap counts in subwords $\mathrm{P_i} u \mathrm{P_{i+1}}$ (represented by $\mathrm{P_1} u \mathrm{P_2}$) and $\mathrm{P_{f_n}} u \mathrm{P_1}$ in words $w_4, \ldots, w_7$. We examine words w_4 and w_5, which are the first even- and odd-numbered words considered in Theorem 4.

- In word w_4, subwords u that separate point $\mathrm{P_1}$ from $\mathrm{P_2}$, and point $\mathrm{P_2}$ from $\mathrm{P_3}$, consist of a single letter L, which is consistent with $f_{4-3} = f_1 = 1$ and $f_{4-4} = f_0 = 0$. Moreover, subword u separating points $\mathrm{P_3}$ and $\mathrm{P_1}$ consists of a single letter S, which is consistent with $f_1 - 1 = 0$ and $f_0 + 1 = 1$.
- For w_5, subwords u separating any pair of points $\mathrm{P_i}$ and $\mathrm{P_{i+1}}$, $i = 1, \ldots, 4$, have one letter L and one letter S, which is consistent with $f_{5-3} = f_2 = 1$ and $f_{5-4} = f_1 = 1$, whereas subword u separating points $\mathrm{P_5}$ and $\mathrm{P_1}$ has 2 letters L and no letter S, which is consistent with $f_2 + 1 = 2$ and $f_1 - 1 = 0$.

Thus Theorem 4 holds for $n = 4$ and $n = 5$.

2. Induction step. We first infer the counts of letters L and S in subwords $\mathrm{P_i} v \mathrm{P_{i+1}} \prec w_{n+1}$, given these counts in subwords $\mathrm{P_i} u \mathrm{P_{i+1}} \prec w_n$. To this end, we consider three cases implied by Lemma 3 for an even n: (1) both priordia $\mathrm{P_i}$ and $\mathrm{P_{i+1}}$ are followed by $\overleftarrow{\mathrm{L}}$ in w_n; (2) $\mathrm{P_i}$ is followed by $\overleftarrow{\mathrm{L}}$, while $\mathrm{P_{i+1}}$ is followed by $\overrightarrow{\mathrm{S}}$; and (3) both $\mathrm{P_i}$ and $\mathrm{P_{i+1}}$ are followed by $\overrightarrow{\mathrm{S}}$. The corresponding cases for an odd n are symmetric and thus do not require separate examination. We then consider the word $\mathrm{P_{f_n}} u \mathrm{P_1}$ as the fourth case, for both even and odd n.

<u>Case 1.</u> For $i = 1, \ldots, f_{n-1} - 1$, points $\mathrm{P_i}$ and $\mathrm{P_{i+1}}$ are both followed by letter $\overleftarrow{\mathrm{L}}$, which results in derivations of the form:

$$\underbrace{\mathrm{P_i}\,\overleftarrow{\mathrm{L}}\,x\mathrm{P_{i+1}}}_{f_{n-3}\mathrm{L}+f_{n-4}\mathrm{S}}\,\overleftarrow{\mathrm{L}} \Rightarrow \underbrace{\mathrm{P_i}\,\overleftarrow{\mathrm{S}}\,\overbrace{\mathrm{P_{i+f_n}}\,\overrightarrow{\mathrm{L}}\,y\,\mathrm{P_{i+1}}}^{f_{n-2}\mathrm{L}+f_{n-3}\mathrm{S}}}_{f_{n-2}\mathrm{L}+f_{n-3}\mathrm{S}}\,\overleftarrow{\mathrm{S}}\,\mathrm{P_{i+1+f_n}}\,\overrightarrow{\mathrm{L}}\,.$$

- According to the inductive hypothesis, subword $\mathrm{P_i}\,\overleftarrow{\mathrm{L}}\,x\mathrm{P_{i+1}} \prec w_n$ has f_{n-3} letters L and f_{n-4} letters S. Each letter L produces letters L and S, while each letter S produces an L, thus subword $\mathrm{P_i} v \mathrm{P_{i+1}} = \mathrm{P_i}\,\overleftarrow{\mathrm{S}}\,\mathrm{P_{i+f_n}}\,\overrightarrow{\mathrm{L}}\,y\mathrm{P_{i+1}} \prec w_{n+1}$ has $f_{n-3} + f_{n-4} = f_{n-2}$ letters L and f_{n-3} letters S.
- Moreover, letters $\overleftarrow{\mathrm{L}}$ preceded by $\mathrm{P_i}$ and $\mathrm{P_{i+1}}$ in w_n produce letters $\mathrm{P_{i+f_n}}$ and $\mathrm{P_{i+1+f_n}}$ that delimit word $\mathrm{P_{i+f_n}} v' \mathrm{P_{i+1+f_n}} = \mathrm{P_{i+f_n}}\,\overrightarrow{\mathrm{L}}\,y\mathrm{P_{i+1}}\,\overleftarrow{\mathrm{S}}\,\mathrm{P_{i+1+f_n}} \prec w_{n+1}$. Ignoring point indices, v' is a permutation of v, thus words $\mathrm{P_{i+f_n}} v' \mathrm{P_{i+1+f_n}}$, $i = 1, \ldots, f_{n-1} - 1$

(after reindexing, $\mathrm{P_i}v'\mathrm{P_{i+1}}$, $i = f_n + 1, \ldots, f_{n+1} - 1$) also have f_{n-2} letters L and f_{n-3} letters S.

Case 2. For $i = f_{n-1}$, point $\mathrm{P_i} = \mathrm{P_{f_{n-1}}}$ in word w_n is followed by an $\overleftarrow{\mathrm{L}}$, but point $\mathrm{P_{i+1}} = \mathrm{P_{1+f_{n-1}}}$ is followed by an $\overrightarrow{\mathrm{S}}$. The resulting derivation thus has the form

$$\underbrace{\mathrm{P_{f_{n-1}}}\,\overleftarrow{\mathrm{L}}\,x\mathrm{P_{1+f_{n-1}}}}_{f_{n-3}\mathrm{L}+f_{n-4}\mathrm{S}}\ \overrightarrow{\mathrm{S}} \Rightarrow \underbrace{\mathrm{P_{f_{n-1}}}\,\overleftarrow{\mathrm{S}}\,\mathrm{P_{f_{n+1}}}\,\overrightarrow{\mathrm{L}}\,y\mathrm{P_{1+f_{n-1}}}}_{f_{n-2}\mathrm{L}+f_{n-3}\mathrm{S}}\ \overrightarrow{\mathrm{L}}\,.$$

This derivation extends the subword separating points $\mathrm{P_{f_{n-1}}}$ and $\mathrm{P_{1+f_{n-1}}}$ to f_{n-2} letters L and f_{n-3} letters S as in Case 1, but does not create an additional subword (point $\mathrm{P_{f_{n-1}+f_n}} = \mathrm{P_{f_{n+1}}}$ is the endpoint of interval $\mathrm{P_i}v'\mathrm{P_{i+1}}$ for $i = f_{n+1} - 1$, and thus was already considered in Case 1). The interval $\mathrm{P_{f_{n+1}}}v\mathrm{P_{f_1}}$ is considered in Case 4.

Case 3. For $i = f_{n-1} + 1, \ldots, f_n - 1$, both points $\mathrm{P_i}$ and $\mathrm{P_{i+1}}$ are followed by letters $\overrightarrow{\mathrm{S}}$. The derivation step extends the subword delimited by points $\mathrm{P_i}$ and $\mathrm{P_{i+1}}$ as in Cases 1 and 2, but no additional subwords are created.

$$\underbrace{\mathrm{P_i}\,\overrightarrow{\mathrm{S}}\,x\mathrm{P_{i+1}}}_{f_{n-3}\mathrm{L}+f_{n-4}\mathrm{S}}\ \overrightarrow{\mathrm{S}} \Rightarrow \underbrace{\mathrm{P_i}\,\overrightarrow{\mathrm{L}}\,y\mathrm{P_{i+1}}}_{f_{n-2}\mathrm{L}+f_{n-3}\mathrm{S}}\ \overrightarrow{\mathrm{L}}\,.$$

Case 4. Taken together, Cases 1–3 show that all subwords $\mathrm{P_i}v\mathrm{P_{i+1}}$ between pairs of consecutively indexed points already present in word w_n have f_{n-2} letters L and f_{n-3} letters S in w_{n+1}. Moreover, Case 1 shows that all subwords $\mathrm{P_i}v\mathrm{P_{i+1}} \prec w_{n+1}$ between pairs of newly inserted points also have f_{n-2} letters L and f_{n-3} letters S. This leaves two subwords of w_{n+1} still requiring analysis: $\mathrm{P_{f_n}}v\mathrm{P_{1+f_n}}$, which relates the sequence of points already present in w_n to the sequence of newly inserted points, and $\mathrm{P_{f_{n+1}}}v'\mathrm{P_1}$, the special case distinguished in part 2 of Theorem 4. It is convenient to consider these subwords together; however, additional reasoning is needed to determine the position of point $\mathrm{P_{f_{n+1}}}$ with respect to $\mathrm{P_1}$ in word w_{n+1}. We proceed by first establishing the position of point $\mathrm{P_{f_{n-1}}}$ with respect to $\mathrm{P_{f_n}}$ in word w_n.

According to the inductive hypothesis, each subword $\mathrm{P_i}u\mathrm{P_{i+1}} \prec w_n$ has f_{n-2} letters L or S. In the circular word w_n, point $\mathrm{P_{i+1}}$ is thus shifted cyclically by f_{n-2} positions (letters L or S) with respect to $\mathrm{P_i}$. It follows that point $\mathrm{P_{f_n}} = \mathrm{P_{f_{n-1}+f_{n-2}}}$ is shifted f_{n-2} times by f_{n-2} positions with respect to $\mathrm{P_{f_{n-1}}}$, which, in terms of modular arithmetic, means that $\mathrm{P_{f_n}}$ has position $f_{n-2}^2 \mod f_n$ relative to $\mathrm{P_{f_{n-1}}}$. To determine this position explicitly, we use Catalan's identity [4,5]:

$$f_n^2 - f_{n-r}f_{n+r} = (-1)^n f_r^2.$$

By substituting $n \leftarrow n-2$ and $r \leftarrow 2$ we obtain $f_{n-2}^2 = (-1)^n + f_{n-4}f_n$, hence $f_{n-2}^2 \equiv 1 \mod f_n$ for an even n. This congruence implies that point $\mathrm{P_{f_n}}$ is separated from $\mathrm{P_{f_{n-1}}}$ by a single letter. By Lemma 3, the letter following $\mathrm{P_{f_n}}$ in word w_n is an $\overrightarrow{\mathrm{S}}$; according to Remarks 1(iii) and 2(iv), the letter preceding $\mathrm{P_{f_n}}$ is thus an $\overleftarrow{\mathrm{L}}$.

In light of this reasoning, we consider the following derivation:

$$\mathrm{P_{f_{n-1}}}\,\overleftarrow{\mathrm{L}}\,\underbrace{\mathrm{P_{f_n}}\,\overrightarrow{\mathrm{S}}\,x\mathrm{P_1}}_{(f_{n-3}-1)\mathrm{L}+(f_{n-4}+1)\mathrm{S}}\,\overleftarrow{\mathrm{L}} \Rightarrow \mathrm{P_{f_{n-1}}}\,\overleftarrow{\mathrm{S}}\,\mathrm{P_{f_{n+1}}}\,\overbrace{\overrightarrow{\mathrm{L}}\,\overbrace{\underbrace{\mathrm{P_{f_n}}\,\overrightarrow{\mathrm{L}}\,y\mathrm{P_1}}_{f_{n-2}\mathrm{L}+(f_{n-3}-1)\mathrm{S}}\,\overleftarrow{\mathrm{S}}\,\mathrm{P_{1+f_n}}}^{(f_{n-2})\mathrm{L}+(f_{n-3})\mathrm{S}}}^{(f_{n-2}+1)L+(f_{n-3}-1)S}\,\overrightarrow{\mathrm{L}}\,.$$

According to the inductive hypothesis, the subword $\mathrm{P_{f_n}}\overrightarrow{\mathrm{S}}x\mathrm{P_1} \prec w_n$ has $f_{n-3}-1$ letters L and $f_{n-4}+1$ letters S. Consequently, the subword $\mathrm{P_{f_n}}\overrightarrow{\mathrm{L}}y\mathrm{P_1} \prec w_{n+1}$ has $(f_{n-3}-1)+(f_{n-4}+1) = f_{n-2}$ letters L and $f_{n-3}-1$ letters S, as indicated by the underbrace in the above diagram. Using this word as a reference, we arrive at two conclusions:

- Subword $\mathrm{P_{f_n}}v\mathrm{P_{1+f_n}} = \mathrm{P_{f_n}}\overrightarrow{\mathrm{L}}y\mathrm{P_1}\overleftarrow{\mathrm{S}}\mathrm{P_{1+f_n}}$ (lower overbrace) has an additional letter $\overleftarrow{\mathrm{S}}$, resulting in f_{n-2} letters L and f_{n-3} letters S in total. This matches the count for all other subwords of w_{n+1} delimited by consecutively indexed points, already considered in Cases 1–3.
- Subword $\mathrm{P_{f_{n+1}}}v'\mathrm{P_1} = \mathrm{P_{f_{n+1}}}\overrightarrow{\mathrm{L}}\mathrm{P_{f_n}}\overrightarrow{\mathrm{L}}\mathrm{P_1}$ (upper overbrace) has an additional letter $\overrightarrow{\mathrm{L}}$, resulting in $f_{n-2}+1$ letters L and $f_{n-3}-1$ letters S, as postulated by Theorem 4 for an odd n.

The analogous derivation for an odd n is slightly different. According to Catalan's identity, in this case $f_{n-2}^2 \equiv -1 \mod f_n$, which implies that point $\mathrm{P_{f_{n-1}}}$ appears after, rather than before, point $\mathrm{P_{f_n}}$:

$$\underbrace{\mathrm{P_{f_n}}\overrightarrow{\mathrm{L}}\mathrm{P_{f_{n-1}}}\overleftarrow{\mathrm{S}}x\overrightarrow{\mathrm{L}}\mathrm{P_1}}_{(f_{n-3}+1)\mathrm{L}+(f_{n-4}+1)\mathrm{S}} \Rightarrow \underbrace{\overbrace{\mathrm{P_{f_n}}\overleftarrow{\mathrm{L}}\mathrm{P_{f_{n+1}}}\overrightarrow{\mathrm{S}}\mathrm{P_{f_{n-1}}}\overleftarrow{\mathrm{L}}y\overleftarrow{\mathrm{L}}\mathrm{P_{1+f_n}}}^{(f_{n-2})\mathrm{L}+(f_{n-3})\mathrm{S}}\overrightarrow{\mathrm{S}}\mathrm{P_1}}_{f_{n-2}\mathrm{L}+(f_{n-3}+1)\mathrm{S}}.$$

$$\mathrm{P_{f_n}}\overleftarrow{\mathrm{L}}\overbrace{\mathrm{P_{f_{n+1}}}\overrightarrow{\mathrm{S}}\mathrm{P_{f_{n-1}}}\overleftarrow{\mathrm{L}}y\overleftarrow{\mathrm{L}}\mathrm{P_{1+f_n}}\overrightarrow{\mathrm{S}}\mathrm{P_1}}^{(f_{n-2}-1)L+(f_{n-3}+1)S}$$

The letter counts in the subwords $\mathrm{P_{f_n}}v\mathrm{P_{1+f_n}}$ and $\mathrm{P_{f_{n+1}}}v'\mathrm{P_1}$, calculated as for an even n, again satisfy the requirement of the inductive step, which concludes the proof. ∎

5. EMERGENCE OF THE GOLDEN ANGLE. L-system (3) and its properties, culminating in Theorem 4, have a topological character: they describe the sequence of primordia and the gaps between them as they arise on the rim of the developing head. To characterize the divergence angle—a geometric feature—let us assume that all gaps L have the same arc length l, and all gaps S have the same arc length s (in general different from l). The same idealization was employed by Zhang et al. [1]. According to Remark 1(i,ii), word w_n, representing the nth stage of patterning, has f_{n-1} letters L and f_{n-2} letters S, so the rim perimeter has a total length $f_{n-1}l + f_{n-2}s$. Moreover, according to Theorem 4, in the same word there are f_{n-3} gaps L and f_{n-4} gaps S between any pair of consecutively indexed primordia $\mathrm{P_i}$ and $\mathrm{P_{i+1}}$, thus the arc of the head perimeter between these primordia has length $f_{n-3}l + f_{n-4}s$. The ratio in which this arc divides the head perimeter is therefore

$$\xi = \frac{f_{n-3}l + f_{n-4}s}{f_{n-1}l + f_{n-2}s} = \frac{f_{n-3}\eta + f_{n-4}}{f_{n-1}\eta + f_{n-2}},$$

where $\eta = l/s$ is the ratio of the gap lengths. Immediately after a burst of primordia insertion, long gaps L have the same length as the short gaps S (Figure 5a). During the subsequent rim expansion, length l increases to $2s$, at which point a new burst of insertion occurs, reducing the length of gaps l to s again. The ratio of gap lengths η thus varies in the range $[\eta_{min}, \eta_{max}) = [1, 2)$. This, in turn, implies that the ratio ξ, in which the arc between consecutively indexed primordia divides the head perimeter, is bounded by

$$\xi_{l=s} = \frac{f_{n-3} + f_{n-4}}{f_{n-1} + f_{n-2}} = \frac{f_{n-2}}{f_n}$$

and

$$\xi_{l=2s} = \frac{2f_{n-3} + f_{n-4}}{2f_{n-1} + f_{n-2}} = \frac{f_{n-3} + f_{n-2}}{f_{n-1} + f_n} = \frac{f_{n-1}}{f_{n+1}}.$$

It is known that the ratios $\frac{f_{n+1}}{f_n}$ of consecutive Fibonacci numbers converge to the golden ratio φ defined by the relation $\varphi = 1 + \varphi^{-1} \approx 1.618$ [4, 5]. As n increases, both ratios $\frac{f_{n-2}}{f_n}$ and $\frac{f_{n-1}}{f_{n+1}}$ thus approximate $\varphi^{-2} \approx 0.382$ (Figure 5b). Specifically, for $\eta = \varphi$, the Fibonacci number property $\varphi^n = f_n\varphi + f_{n-1}$ [4, 5] implies that the arc between consecutively indexed primordia partitions the head rim exactly in the ratio $\xi_{l=\varphi s} = \frac{\varphi^{n-3}}{\varphi^{n-1}} = \varphi^{-2}$, independently of the developmental stage n. Interestingly, this ratio holds even for non-circular (fasciated) heads [20]. In the typical case of circular heads, expressing ratio $\xi_{l=\varphi s}$ as a fraction of the full angle yields the golden divergence angle $\theta = 360°\varphi^{-2} \approx 137.5°$ (Figures 5b and 6).

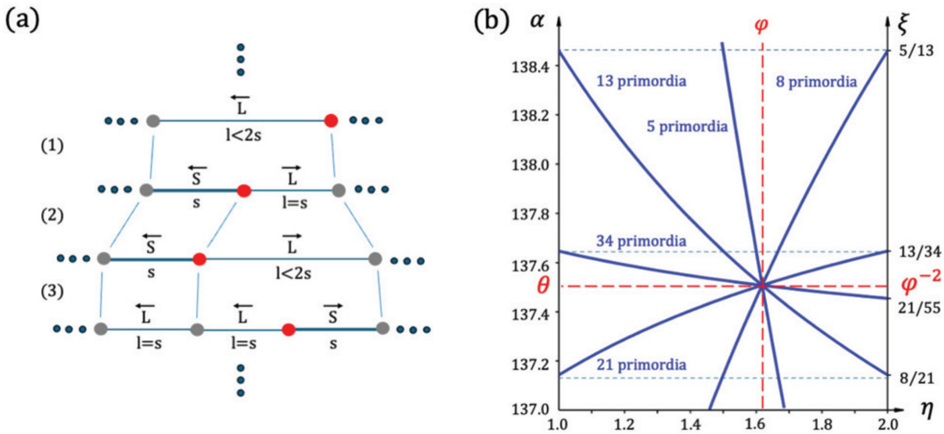

Figure 5. Geometry of primordia patterning on the rim. (a) Dynamics of primordia insertion. (1) A new primordium is inserted into a long gap when its length reaches twice the minimum gap length s. (2) During the subsequent rim expansion, the new primordium remains close to its older neighbor, while the long gap elongates. The gap length ratio $\eta = \frac{l}{s}$ gradually increases from 1 to 2. (3) A new primordium is inserted into the long gap, bringing η back to 1. (b) The ranges of the divergence angle α predicted by the model for 5 to 34 primordia on the rim. The admissible ranges become smaller as the number of primordia increases. When the ratio of long to short gap lengths η equals the golden ratio φ, the divergence angle is equal to the golden angle θ independently of the number of primordia. The axis ξ indicates the ratios at which the arc between consecutively indexed primordia divides the head rim.

6. DISCUSSION. We proceeded from experimental results to a developmental model capturing the essence of phyllotactic patterning in flower heads, then used this model to derive one of the most intriguing properties of phyllotaxis: the emergence of the golden angle. A critical element of this path of reasoning was the observation of the asymmetric displacement of incipient primordia toward their older neighbors on the growing head rim [1]. This observation, enabled by recent molecular-level microscopy techniques, was not available to earlier researchers, which helps explain why the question of the emergence of the golden angle in flower heads has long

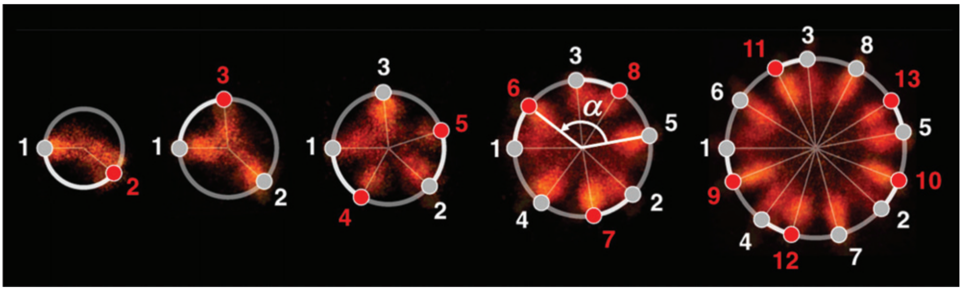

Figure 6. Revisiting the pattern of primordia on a developing Gerbera head (see Figure 2). With primordia indexed according to L-system (3), the divergence angle α between consecutively indexed primordia (highlighted in one example) closely approximates the golden angle.

remained unsettled. Nevertheless, while not addressing causality, several results connecting the patterning of primordia on the head rim to the golden angle had been obtained by assuming the golden angle as given. Specifically, Max Hirmer conjectured [**21**], and Johannes Battjes and Przemyslaw Prusinkiewicz proved [**22**], that the maximum number of primordia which can then be placed without intersections on a circle is—for any fixed primordium size—a Fibonacci number. Inspired by Hirmer's conjecture, Battjes et al. [**23**] documented and analyzed the one-dimensional phyllotactic pattern on the head rim in *Microseris pygmaea* (another plant in the Aster family), and Fowler et al. [**24**] proposed a computational model of phyllotaxis applicable to diverse plants. Analyzing the pattern of gaps in the context of the celebrated three-gap theorem (Steinhaus conjecture), van Ravenstein et al. described the same pattern of short and long gaps as that generated by L-system (2) [**25**, **26**]. The advancement presented here may provide an opportunity to synthesize these results.

As mentioned earlier, the one-dimensional pattern of primordia separated by long and short gaps serves as a template upon which a lattice-like two-dimensional pattern of intersecting parastichies subsequently develops. Zhang et al. [**1**] demonstrated this 1D-to-2D progression using simulations, but its mathematical analysis would also be of interest as an instance of the nontrivial relation between periodic lattices and aperiodic structures at their boundary. While this relation is the essence of the projection method for constructing aperiodic patterns on the basis of periodic lattices [**27**], it appears that, in the phyllotactic patterning of flower heads, nature acts in the opposite direction, constructing a lattice of primordia on the basis of an aperiodic pattern on the rim. Further analysis of this process would also clarify connections to the classic lattice-based theory of phyllotaxis [**2**, **28**], which is focused on two-dimensional patterns.

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