Packing efficiency in sunflower heads

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Packing Efficiency in Sunflower Heads

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ABSTRACT

In the mathematical description given by Vogel [1], the seeds on a sunflower head are centered at points on a "cyclotron spiral," with constant divergence angle between any two successive seeds. It is shown that the divergence angle occurring in nature (and leading to the appearance of the Fibonacci numbers) gives the theoretically most efficient packing of the seeds. The inadequacy of Vogel's explanation for the occurrence of the Fibonacci angle is also discussed.

INTRODUCTION

Vogel's model for the sunflower capitulum [1] has the seeds centered at the points of the primary growth spiral $\{\sqrt{n}\, \exp 2\pi ni\delta \mid n = 1,2,3,\dots\}$, where $\delta = g^2$, and g is the golden mean, i.e. $g = \frac{1}{2}(\sqrt{5}-1)$, so that $g^2 = 1 - g = 1/(2+g)$. This model is based on two assumptions:

(i) the seeds have equal area (which we take to be π, the area of a disc of radius 1);

(ii) any two successive seeds subtend the same angle ($2\pi\delta$ radians) at the origin.

From the first assumption it follows that the central portion of the capitulum, containing the n youngest seeds, has area $n\pi$, and therefore has radius $\sqrt{n}$. The nth seed, being on the periphery of this region, lies at a distance $\sqrt{n}$ from the origin. By the second assumption, the angular coordinate of the nth seed is $2\pi n\delta + c$, where c is a constant that can be put equal to zero without loss of generality. The model describes all the features visible in actual composite capitula, especially those concerned with the "secondary arcs" or *parastichies*, where each q-parastichy consists of all points for which n belongs to a particular congruence class modulo q. The primary growth spiral is thus the unique 1-parastichy.

The main purpose of this paper is to show that if δ is any number other than g^2 in the interval $[0, \frac{1}{2}]$, then the resulting configuration will provide a less efficient way of packing the seeds in the plane, in a sense to be made precise later. The angle $2\pi\delta$ is called the *divergence angle*, and the *Fibonacci angle* is the optimum divergence angle, i.e. $2\pi g^2 \approx 137.5°$.

In the final section the deficiencies in Vogel's attempt to justify the occurrence of the Fibonacci angle are pointed out, and the most likely explanation mentioned. This is *not* based on packing efficiency, in spite of the result obtained in this paper.

PACKING EFFICIENCY

A countably infinite subset X of the plane will be said to provide an *equal-area packing* if the number of points of X lying inside the circle $|z| = \rho$ is asymptotically equal to $\pi\rho^2/A$ as $\rho \to \infty$, for some constant A, which can be thought of as the *average area* of the region occupied by each point. More precisely,

$$A = \lim_{\rho \to \infty} \frac{\pi\rho^2}{\#\{x \in X : |x| < \rho\}}.$$

For example, any regular lattice $\{m\alpha + n\beta \,|\, m, n \in \mathbb{Z}\}$, where α and β are fixed complex numbers and α/β is not real, provides an equal-area packing with A equal to the area of the parallelogram with vertices $0, \alpha, \beta, \alpha+\beta$. Similarly, the primary growth spiral above, for any divergence angle, provides an equal-area packing with $A = \pi$, since the disc $|z| \leqslant \rho$ contains $[\rho^2]$ points of the spiral. (This is the basis of Vogel's "lateral growth program" [1, p. 181].)

If a set X provides an equal-area packing, then globally its points are evenly distributed in the plane. Locally, however, the situation may be very different: the points may be densely packed in some regions and sparse in others. We shall regard the packing as *efficient* if this local variation is small.

One way to measure efficiency is to use the infimum of the squares of the distances between distinct points in X. If this infimum is large, relative to A, then there are no densely packed regions, and consequently (because of the equal-area assumption) no sparse regions either. We therefore define the *normalized packing efficiency* η of a set X as

$$\eta = A^{-1} \inf\{|x-y|^2 : x, y \in X, x \neq y\},$$

provided that the limit A exists. Larger values of η correspond to more efficient packings.
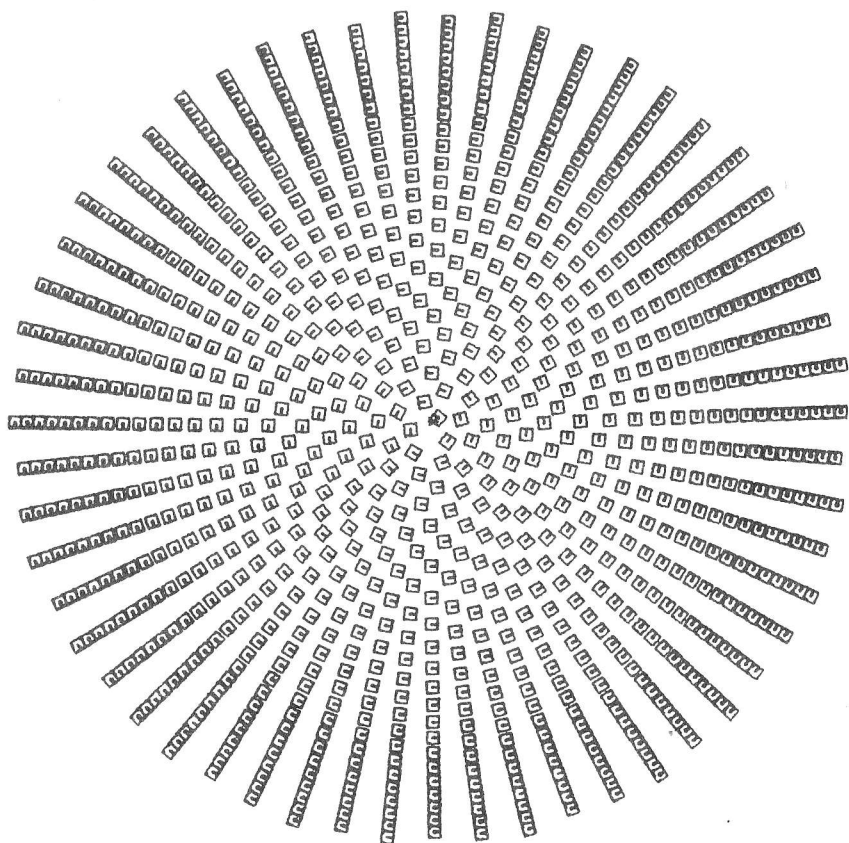
FIG. 1. A rational approximation to the Fibonacci angle.

The figures, drawn on a Calcomp plotter, represent three capitula with divergence angles near the Fibonacci angle. In Figure 1, with $\delta = \frac{21}{55}$, the center is evenly covered, but further out the seeds concentrate on the 55-parastichies like spokes on a wheel. Adjacent seeds on any one spoke become arbitrarily close together sufficiently far from the origin, so η for the infinite capitulum is in fact zero. In Figure 2, with $\delta = (155 + \sqrt{13})/414$, the seeds accumulate visibly, first on the 13-parastichies and then on the 47-parastichies. These will be replaced by the 154- and higher parastichies at greater distances from the origin. The seeds never approach arbitrarily closely, so η is nonzero, but small (less than 0.56). In Figure 3, with $\delta = g^2$, the seeds cover the whole disc evenly; there are no close juxtapositions, and η is relatively high (approximately 0.8169). In fact $\eta = (5 - 4\cos 6\pi g^2)/\pi$, which we shall show is the maximum value attained for these spiral packings.
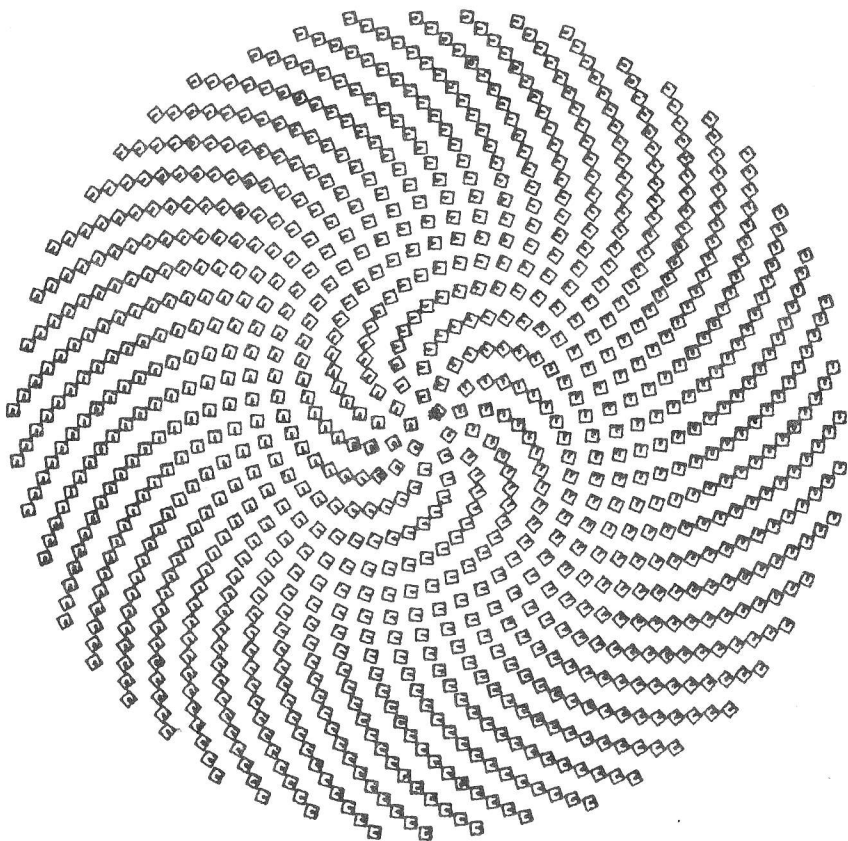
FIG. 2.   An irrational approximation to the Fibonacci angle.

It is of interest to compare this optimum value of η with the efficiencies of regular rhombic lattices. We therefore consider the set

$$\{m + n \exp i\theta : m, n \in \mathbb{Z}\},$$

where we may assume that $0 < \theta \leqslant \pi/2$. The fundamental region is a rhombus with sides of length 1 and acute angle θ, so the area $A = \sin \theta$. The minimum distance between distinct points is the length of either one side or the shorter diagonal, i.e. $\min\{1, 2\sin\frac{1}{2}\theta\}$, which is 1 if $\theta \geqslant \pi/3$ and is $2\sin\frac{1}{2}\theta$ if $0 < \theta \leqslant \pi/3$. Hence $\eta = 1/\sin \theta = \csc \theta$ for $\pi/3 \leqslant \theta \leqslant \pi/2$, and $\eta = (4\sin^2\frac{1}{2}\theta)/(\sin\theta) = 2\tan\frac{1}{2}\theta$ for $0 < \theta \leqslant \pi/3$. Thus η has a maximum value of $2/\sqrt{3}$, which is attained when $\theta = \pi/3$, i.e. the hexagonal close packing, as one would expect. It also follows that these rhombic packings are more
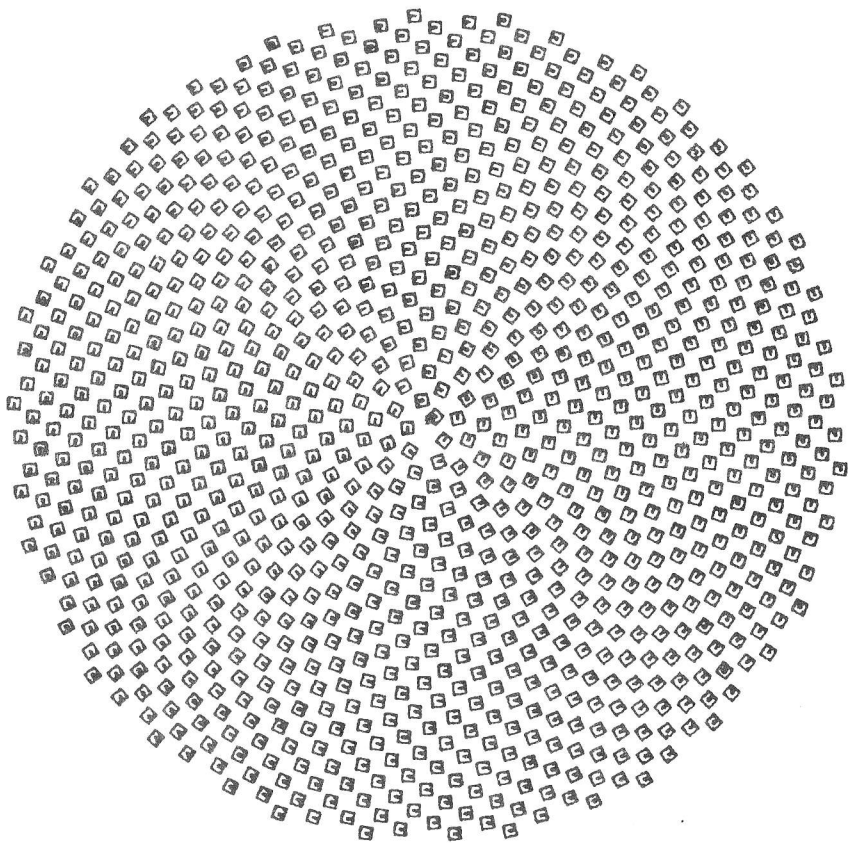
FIG. 3.   The Fibonacci angle.

efficient than the best spiral one when $2\tan\frac{1}{2}\theta \geq (5-4\cos 6\pi g^2)/\pi$, i.e. $\theta \geq 44\frac{1}{2}°$ approximately.

THE MAIN THEOREM

THEOREM

If $X = \{\sqrt{n}\exp 2\pi ni\delta : n = 1, 2, 3, \ldots\}$, where $0 \leq \delta \leq \frac{1}{2}$, then $\eta \leq (5-4\cos 6\pi g^2)/\pi$. This maximum value is achieved if and only if $\delta = g^2$.

Proof. If $d = d(n, m)$ denotes the distance between the mth and nth seeds, then

$$d^2 = m + n - 2\sqrt{mn}\cos 2\pi(m-n)\delta.$$

For convenience we put $t = m + n$ and $q = |m - n|$, and let $\beta = 2\pi|q\delta - p|$, where p is the nearest integer to $q\delta$, so that $0 \leqslant \beta \leqslant \pi$. The seeds then lie on a q-parastichy (since $m \equiv n$ modulo q), and $d^2 = t - (t^2 - q^2)^{1/2}\cos\beta$; we wish to find the minimum value of d^2, since $\eta = \inf(d^2)/\pi$. The rest of the proof is contained in four lemmas.

LEMMA 1

If $0 < \beta < \pi/2$, then on one of the q-parastichies d^2 attains a minimum value that lies between $q\sin\beta$ and $q\sin\beta(1 + 2q^{-2}\tan^2\beta)$. If $\beta \geqslant \pi/2$, then the minimum value of d^2 on the q-parastichies is $d^2(1, 1+q)$. If $\beta = 0$, then $d^2 \to 0$ as $t \to \infty$.

Proof. We have $d^2 = t - (t^2 - q^2)^{1/2}\cos\beta = f(t)$ say, where we temporarily regard t as a continuous variable (and q and β are fixed). If $\beta \geqslant \pi/2$, then $\cos\beta \leqslant 0$, so $f(t)$ increases with t. If $\beta = 0$ (i.e. if δ is a rational number with denominator dividing q), then $f(t) = q^2/[t + (t^2 - q^2)^{1/2}]$, which tends to 0 as $t \to \infty$. Finally, if $0 < \beta < \pi/2$, then from elementary calculus it follows that $f(t)$ has a minimum value $q\sin\beta$, attained at $t = q\csc\beta$. At this minimum point $f''(t) = q^{-1}\sin\beta\tan^2\beta$, and f'' is a decreasing function, since $f'''(t) < 0$ for all $t > q$. Hence if $t \geqslant q\csc\beta$, then by the second mean-value theorem we have

$$f(t) \leqslant f(q\csc\beta) + \tfrac{1}{2}(t - q\csc\beta)^2 f''(q\csc\beta)$$
$$= q\sin\beta\left\{1 + \tfrac{1}{2}(t - q\csc\beta)^2 q^{-2}\tan^2\beta\right\}.$$

Since in fact t is not continuous, but assumes only integer values congruent to q modulo 2, there is an acceptable value of t such that $0 \leqslant t - q\csc\beta < 2$, which gives the required result.

LEMMA 2

For any δ, the minimum value (if any) of d^2 occurs on a q-parastichy, where q is the denominator of a continued fraction convergent to δ.

Proof. Suppose $q_i < q < q_{i+1}$, where p_i/q_i and p_{i+1}/q_{i+1} are consecutive convergents to δ; let $\beta_i = 2\pi|q_i\delta - p_i|$ and $f_i(t) = t - (t^2 - q_i^2)^{1/2}\cos\beta_i$, i.e. the distance-squared function on the q_i-parastichies. From the theory of continued fractions (see e.g. [2], in the proof of Theorem 182, or [3, Theorem 7.13]), we have $\beta_i < \beta$, so $\cos\beta_i > \cos\beta$. Since also $t^2 - q_i^2 > t^2 - q^2$, it follows that $f_i(t) < f(t)$ for all $t \geqslant q$. If $q_i \equiv q$ modulo 2, then acceptable values of t for the functions f and f_i coincide, so $f(t)$ can never be the minimum value of d^2.

If $q_i \not\equiv q$ modulo 2, and if t is acceptable for f, then $t-1$ and $t+1$ are acceptable for f_i. If either $f_i(t-1) < f(t)$ or $f_i(t+1) < f(t)$, then again $f(t)$ cannot be the minimum value of d^2.

There remains the possibility that $f_i(t_0 - 1) \geqslant f(t_0)$ and $f_i(t_0 + 1) \geqslant f(t_0)$ for some t_0 acceptable for f, i.e. such that $t_0 \geqslant q+2$ and $t_0 \equiv q$ modulo 2. Since $f_i(t) \leqslant f(t)$ for all t, it follows that the functions f and f_i must both have minimum turning points on the interval $[t_0 - 1, t_0 + 1]$. Hence by Lemma 1 $q_i \csc \beta_i \geqslant t_0 - 1$, but $t_0 \geqslant q+2$ and $q \geqslant q_i + 1$, so in fact

$$q_i \csc \beta_i \geqslant q_i + 2. \tag{1}$$

Also, by Lemma 1, $f(t_0) \geqslant q \sin \beta$ and $f_i(t_0 + 1) \leqslant q_i \sin \beta_i (1 + 2 q_i^{-2} \tan^2 \beta_i)$. Moreover, $f(t_0) \leqslant f_i(t_0 + 1)$, and $q \geqslant q_i + 1$, and $\sin \beta \geqslant \sin \beta_i$ (since $\beta > \beta_i$, and both lie between 0 and $\pi/2$ because f and f_i have minimum turning points), so $q_i + 1 \leqslant q_i + 2 q_i^{-1} \tan^2 \beta_i$, whence

$$q_i \cot^2 \beta_i \leqslant 2. \tag{2}$$

From (1) and (2) and the identity $\csc^2 \theta = 1 + \cot^2 \theta$, it follows that $(q_i + 2)^2 \leqslant q_i^2 + 2 q_i$, which is an obvious contradiction.

LEMMA 3

   If $\delta = g^2$, then the minimum value of d^2 is $d^2(1,4) = 5 - 4\cos 6\pi g^2 = c$ say.

Proof. The convergents to g^2 are F_{i-2}/F_i for $i = 2,3,4 \ldots$, where F_i is the ith Fibonacci number, i.e. $F_0 = 0$, $F_1 = 1$, and $F_i = F_{i-2} + F_{i-1}$ for $i \geqslant 2$. It is well known [3, p. 101] that $F_i = [g^{-i} - (-g)^i]/\sqrt{5}$, whence $|F_i g^2 - F_{i-2}| = g^i$, and $\beta_i = 2\pi g^i$. If $i \geqslant 3$, then $\beta_i < \pi/2$, so, by Lemma 1, on the F_i-parastichies

$$d^2 \geqslant F_i \sin \beta_i$$
$$\geqslant F_i \beta_i \left(1 - \beta_i^2/6\right)$$
$$\geqslant \frac{2\pi}{\sqrt{5}} (1 - g^{2i}) \left(1 - \frac{2\pi^2 g^{2i}}{3}\right)$$
$$\geqslant \frac{2\pi}{\sqrt{5}} \left[1 - \left(1 + \frac{2\pi^2}{3}\right) g^{2i}\right]$$
$$> c \quad \text{if} \quad i \geqslant 5, \text{ i.e. } F_i \geqslant 5 \text{ also.}$$

The parastichies that remain to be considered correspond to $q = 1$, 2, and 3. On the 1-parastichy $d^2 \geqslant d^2(1,2) > c$, on the 2-parastichies $d^2 \geqslant d^2(1,3) > c$, and on the 3-parastichies $d^2 \geqslant d^2(1,4) = c$, which is the overall minimum value.

LEMMA 4

If $\delta \neq g^2$, then $d^2(m, n) < c$ for suitable m and n.

Proof.   The essence of the proof is that if $|q\delta - p|$ is sufficiently small, then the minimum value of d^2 attained on a q-parastichy will be less than c. This provides an open interval with center p/q, such that, for every value of δ in that interval, $d^2(m, n) < c$ for suitable m and n differing by q. We find a family of such intervals that covers all of $[0, \frac{1}{2}]$ except for the point g^2.

Case i: $0 \leq \delta < g^2$.   We consider $q = 1, 4, 3$. Direct calculation shows that $d^2(1,2) < c$ if $|\delta| < 0.2254\ldots$, that $d^2(1,5) < c$ if $|\delta - \frac{1}{4}| < 0.0276\ldots$, and that $d^2(1,4) < c$ if $|\delta - \frac{1}{3}| < g^2 - \frac{1}{3} = 0.0486\ldots$. At least one of these inequalities holds for every δ in $[0, g^2)$.

Case ii: $\frac{2}{5} \leq \delta \leq \frac{1}{2}$.   Considering $q = 5$ and $q = 2$, we obtain $d^2(2,7) < c$ if $|\delta - \frac{2}{5}| < 0.0170\ldots$, and $d^2(1,3) < c$ if $|\delta - \frac{1}{2}| < 0.0910\ldots$. At least one of these two inequalities holds for every δ in $[\frac{2}{5}, \frac{1}{2}]$.

Case iii: $g^2 < \delta \leq \frac{2}{5}$.   We prove that if

$$\frac{F_{2i+1}}{F_{2i+3}} \leq \delta \leq \frac{F_{2i-1}}{F_{2i+1}}$$

for $i \geq 2$, then $d^2(m, n) < c$ somewhere on one of the F_{2i+1}-parastichies. These intervals then cover $(g^2, \frac{2}{5}]$. Under the given hypothesis, putting $q = F_{2i+1}$, we obtain

$$\beta = 2\pi |F_{2i+1}\delta - F_{2i-1}|$$
$$\leq 2\pi |(F_{2i+1})^2 - F_{2i-1}F_{2i+3}| / F_{2i+3}$$
$$= 2\pi / F_{2i+3} \qquad \text{since} \quad (F_{2i+1})^2 - F_{2i-1}F_{2i+3} = -1$$
$$\leq 2\pi / 13.$$

Hence $2 \tan^2 \beta < 1$, and furthermore

$$q \sin \beta \leq q\beta \leq 2\pi F_{2i+1} / F_{2i+3} \leq 10\pi / 13.$$

It follows from Lemma 1 that on the q-parastichies the minimum value of d^2 is at most

$$\frac{10\pi}{13}(1 + 13^{-2}) < c.$$

This completes the proof of the lemma, and the theorem.

CONSEQUENCES OF THE THEOREM

It can be shown that if one considers separately the regions lying outside and inside the circle $|z| = \rho$, then in the exterior annulus the most efficient spiral packing is still provided by $\delta = g^2$. The efficiency here approaches $2/\sqrt{5} = 0.8944\ldots$ as $\rho \to \infty$, but any other δ of the form $(p + qg)/(r + sg)$ with $ps - qr = \pm 1$ provides a packing that approaches the same limiting efficiency, although more slowly than for $\delta = g^2$. If δ is not of the above form, then the limiting efficiency in the exterior annulus is at most $1/\sqrt{2}$. These results follow from the discussion in [2, pp. 163–166], since by Lemma 1 the limiting efficiency is

$$\pi^{-1} \liminf_{q \to \infty} q \sin 2\pi |q\delta - p| = 2 \liminf_{q \to \infty} q|q\delta - p|.$$

In contrast, in the interior of the disc there *are* slightly more efficient spiral packings than that provided by g^2. If $\delta > g^2$, then $3\delta - 1 > 3g^2 - 1$, so in the δ-spiral $d^2(1,4) > c$. The points in the δ-spiral for which $d^2 < c$ (as described in Lemma 4, case iii) will lie outside the circle $|z| = \rho$ if δ is sufficiently close to g^2.

A consequence of Lemma 2 is that the number of parastichies that are conspicuous at a particular distance from the center is always the denominator of a convergent to δ. The reason is that conspicuous parastichies are determined by nearest neighbors; by Lemma 2 nearest neighbors lie on a q_i-parastichy, where q_i is the denominator of a convergent to δ; and there are precisely q_i distinct q_i-parastichies. If two successive denominators q_{i-1} and q_i can be found in this way, then all convergents up to p_i/q_i can be determined. For let $a_i = [q_i/q_{i-1}]$; then $q_{i-2} = q_i - a_i q_{i-1}$, and the process can be repeated, terminating as soon as it reaches $1 = q_0$. Then $p_0 = 0$, $p_1 = 1$, and $p_j = a_j p_{j-1} + p_{j-2}$, so the numerators up to p_i can now be calculated. This determines δ with an absolute error of at most $1/q_i q_{i-1}$. For example, with the capitulum in Figure 2, in which the 13- and 47-parastichies are conspicuous, it can be shown in this way that δ lies between $\frac{5}{13}$ and $\frac{18}{47}$.

VOGEL'S EXPLANATION FOR THE FIBONACCI ANGLE

Vogel [1, p. 181] notes the fact that if δ_n is rational, say $\delta_n = p_n/q_n$, then the q_n-parastichies radiate straight out from the center, leaving unfilled gaps between them, which is obviously inefficient. He claims that this is best remedied by replacing δ_n with δ_{n+1}, where

$$\delta_{n+1} = \frac{p_{n+1}}{q_{n+1}} = \delta_n \left(1 - q_n^{-2}\right)^{-1},$$

and then letting $n \to \infty$. The above relation between δ_n and δ_{n+1} leads to the equation

$$\delta_{n+1} = \delta_0 \prod_{i=0}^{n} \left(1 - q_i^{-2}\right)^{-1},$$

and the infinite product converges for any rational δ_0 in $(0, 1)$, so the process does lead to a limiting value, say δ. If $\delta_0 = \frac{1}{3}$, then $\delta = g^2$, which Vogel regards as a complete explanation of why the Fibonacci angle occurs in nature.

The following flaws in the argument are easily detectable, however:

(i) If the initial value δ_0 is not of the form F_{2k}/F_{2k+2}, then the limit δ is not g^2. Thus this procedure does not explain the almost universal occurrence of Fibonacci phyllotaxis for divergence angles between $2\pi/3$ and π.

(ii) If $\delta_0 = \frac{1}{4}$, then Vogel's formula leads to $\delta = 2 - \sqrt{3}$, whereas in nature divergence angles between $\pi/2$ and $2\pi/3$ most commonly exhibit phyllotactic patterns based on the Lucas numbers [3, p. 148], which require $\delta = 1/(3 + g)$.

(iii) The particular procedure used to give the improvement δ_{n+1} in terms of δ_n is completely arbitrary. Other equally plausible ones can easily be devised; the only apparent reason for choosing this one is that (if the initial value δ_0 is carefully selected) it does lead to the limit $\delta = g^2$.

(iv) No biological mechanism is suggested by which the divergences are adjusted in nature.

This final weakness is most important, because to provide a satisfactory explanation for Fibonacci phyllotaxis it is not sufficient to find some mathematical property of g^2 that makes $2\pi g^2$ the optimum divergence angle. What is really essential is a plausible biological criterion with respect to which the florets (or seeds) will be perturbed in such a way as to make the divergences tend to g^2. For, while it is reasonable to assume that the plant could contain genetic information determining the divergence angle to some extent, it is completely impossible for this alone to fix the divergence angle to the incredible accuracy occurring in nature, since natural variation in biological phenomena is normally rather wide. For example, for the 55- and 89-parastichies to be conspicuous, as occurs in most sunflower heads, δ must lie between $\frac{21}{55}$ and $\frac{34}{89}$, a relative accuracy of one part in 1869.

In fact, explanations for Fibonacci phyllotaxis are extremely complicated, and the riddle is by no means completely solved; Adler's contact-pressure model [4, 5] is the most satisfactory one to date. Computer experiments are in progress to find out whether simulated contact pressure alone can perturb random initial divergence angles so as to make their mean tend to $2\pi g^2$ and their variance to zero.

In view of the main theorem of this paper it might seem that packing efficiency could provide a criterion explaining Fibonacci phyllotaxis (i.e. after the birth of each new floret, all existing florets are perturbed in order to improve the packing efficiency, thereby moving the divergence angles nearer $2\pi g^2$). However, from computer calculations it is clear that packing efficiency fluctuates so wildly with changes in the divergence angle that it can only be regarded as a consequence, not a cause, of Fibonacci phyllotaxis.

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