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On geodesics of phyllotaxis

Roland Bacher

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*Abstract*¹: Seeds of sunflowers are often modelled by the map $n \mapsto \varphi_\theta(n) = \sqrt{n}e^{2i\pi n\theta}$ leading to a roughly uniform repartition with two consecutive seeds separated by the divergence angle $2\pi\theta$ for θ the golden ratio. We associate to an arbitrary real divergence angle $2\pi\theta$ a geodesic path $\gamma_\theta : \mathbb{R}_{>0} \rightarrow \mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$ of the modular curve and use it for local descriptions of the image $\varphi_\theta(\mathbb{N})$ of the phyllotactic map φ_θ .

Given a real parameter θ , we call the map $\varphi_\theta : \mathbb{N} \rightarrow \mathbb{C}$ defined by

$$\varphi_\theta(n) = \sqrt{n}e^{2i\pi n\theta}$$

the *phyllotactic map of divergence angle $2\pi\theta$* (measured in radians). The image $\varphi_\theta(\mathbb{N})$ of a phyllotactic map is the *phyllotactic set* (of parameter θ or divergence angle $2\pi\theta$). A phyllotactic set $\varphi_\theta(\mathbb{N})$ is uniformly discrete (i.e. two distinct elements of $\varphi_\theta(\mathbb{N})$ are at distance at least ϵ for some strictly positive ϵ) with uniform density if

$$\theta = [a_0; a_1, a_2, \dots] = a_0 + \frac{1}{a_1 + \frac{1}{a_2 + \dots}}$$

is irrational with bounded coefficients a_0, a_1, a_2, \dots in its continued fraction expansion.

Among all possible parameters, the value given by the golden ratio $\frac{1+\sqrt{5}}{2} = [1; 1, 1, 1, \dots]$ (or closely related numbers) stands out and gives a particularly nice configuration. Figure 1 displays a few hundred small points of $\varphi_{(1+\sqrt{5})/2}(\mathbb{N})$.

Finite approximations of $\varphi_{(1+\sqrt{5})/2}(\mathbb{N})$ can be observed in capitula (heads) of sunflowers or daisies (the map $\varphi_{(1+\sqrt{5})/2}$, sometimes also called the sunflower-map, has been proposed in [13] as a model for heads of sunflowers). Joining close points of $\varphi_{(1+\sqrt{5})/2}(\mathbb{N})$ we get *parastichy spirals* appearing in pairs of crisscrossing families enumerated by two consecutive elements of the Fibonacci sequence $1, 2, 3, 5, 8, 13, 21, \dots$. Explaining the occurrence of the

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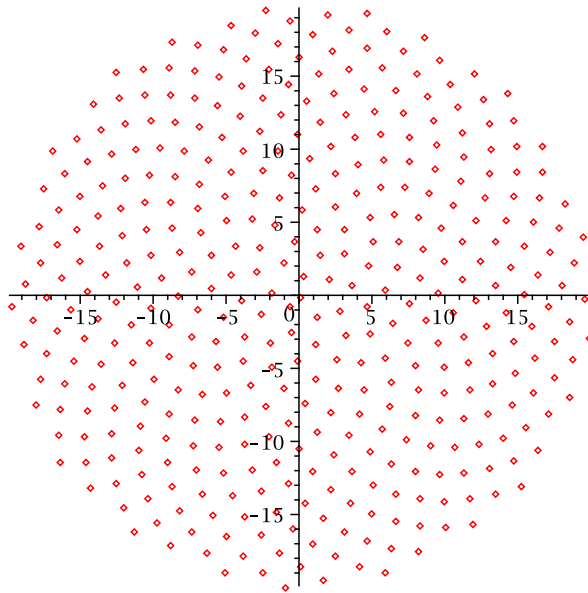


Figure 1: All points of $\varphi_{(1+\sqrt{5})/2}(\mathbb{N})$ in the disc $\{z \in \mathbb{C} \mid |z| \leq 20\}$.

golden ratio and of Fibonacci numbers in Botany is the goal of Phyllotaxis, see for example Chapter XIV of [12] or [6] for more recent developments. The aim of this paper is to describe an elegant framework involving hyperbolic geometry. The emergence of the golden ratio $\frac{1+\sqrt{5}}{2}$ (or of closely related numbers) and of Fibonacci numbers enumerating families of parastichy spirals is then a consequence of natural constraints.

Reasons for Phyllotaxis should be separated from the mechanisms which are involved. How Phyllotaxis works is surely best addressed by biologists, biochemists or biophysicists. The reason for Phyllotaxis is efficiency of some sort (a precise definition is perhaps not so easy) which can take several forms. It is perhaps a physical notion like energetic efficiency or it involves geometric quantities like isoperimetry (which leads probably ultimately also to some kind of energetic efficiency). The link between the two aspects is natural selection. To say it in a nutshell, ubiquity of phyllotaxis involves mathematics: A few geometric configurations optimize some natural quantities. Thus they are favoured by living organisms through natural selection.

Interestingly, the two aspects are spatially separated: Reasons for Phyllotaxis, due to a globally optimized quantity, are of an asymptotical nature. They are best addressed by studying the large part of a plant which is relatively far from the center consisting of the bud which is responsible for the growth-process of a flower. Asymptotic arguments are thus not a weakness but are relevant when trying to answer why phyllotaxis occurs (assuming Darwin's theory of evolution).

An outline of the paper is as follows: We associate to a phyllotactic map φ_θ with real parameter $\theta \in [0, 1)$ the curve

$$(0, +\infty) \ni t \mapsto \gamma_\theta(t) = \frac{4i\pi t}{4i\pi\theta t + 1} = \frac{16\pi^2\theta t^2 + 4i\pi(1 - \theta)t}{16\pi^2\theta^2 t^2 + 1}$$

of the Poincaré halfplane $\mathbb{H} = \{z \in \mathbb{C} \mid \Im(z) > 0\}$. Since $\varphi_\theta = \varphi_{\theta+n}$ for all $n \in \mathbb{Z}$, we extend the definition of γ_θ to $\theta \in \mathbb{R}$ by setting

$$\gamma_\theta(t) = \frac{4i\pi t}{4i\pi\{\theta\}t + 1}$$

where $\theta = [\theta] + \{\theta\}$ with $[\theta] \in \mathbb{Z}$ and $\{\theta\} \in [0, 1)$ denoting the integral and fractional part of θ . It is easy to check that γ_θ defines a geodesic with respect to the usual hyperbolic metric of \mathbb{H} . We call γ_θ the *phyllotactic geodesic* associated to φ_θ . For large $N \in \mathbb{N}$, the projection of $\gamma_\theta(N)$ (often identified with $\gamma_\theta(N)$ in the sequel) onto the modular curve $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$ classifying complex lattices up to similarity describes, up to an affine orientation-preserving similarity, the affine lattice obtained by “linearizing” the phyllotactic map φ_θ in a neighbourhood of $\varphi_\theta(N)$. Linearization is an asymptotical construction involving an error of order $O\left(\frac{1}{\sqrt{N}}\right)$ in a neighbourhood of a point $\varphi_\theta(N)$. In particular, it breaks down for very small values of N . This failure should have no serious consequences: Indeed, the most interesting phyllotactic sets have obviously already good packing properties at their center. Moreover, the center yields a very small contribution to interesting quantities like energy, mean isoperimetric values of Voronoi domains etc..

The apparition of the golden ratio $\frac{1+\sqrt{5}}{2}$ can now be explained by the fact that the corresponding phyllotactic geodesic $t \mapsto \frac{4i\pi t}{2i\pi(-1+\sqrt{5})t+1}$ avoids the cusp of the modular curve $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$. This ensures small excentricity (or, equivalently, good isoperimetric constants) for Voronoi domains of the phyllotactic set $\varphi_{(1+\sqrt{5})/2}(\mathbb{N})$ where the Voronoi domain V_v of a point $v \in S$ with respect to a discrete set S in a metric space E is the subset $V_v = \{x \in E \mid d(x, v) = \min_{y \in S} d(x, y)\}$ of all points closest to v . Plants having seed-areas with good isoperimetric constants should be favoured by natural selection since they need less material for constructing seed coats around seeds of given volume. Thus, Diophantine properties of the golden ratio $\tau = \frac{1+\sqrt{5}}{2}$ ensure that $\varphi_\tau(\mathbb{N})$ (or $\varphi_\theta(\mathbb{N})$ for θ a close relative of the golden ratio τ giving rise e.g. to the sequence 1, 3, 4, 7, 11, 18, ... also observed in Phyllotaxis) satisfies natural constraints in the class of all sets of the form $\varphi_\theta(\mathbb{N})$.

We can either consider that the points of the sequence $\varphi_\theta(0), \varphi_\theta(1), \dots$ appear sequentially with constant divergence angle $2\pi\theta$ between consecutive points on the so-called *ontogenetic spiral* $t \mapsto \sqrt{t}e^{2i\pi\theta t}$ or, sticking perhaps closer to biological reality, we can consider a sequence of paths $[-n, 0] \ni t \mapsto s_{n,\theta}(t) = \sqrt{n+te^{2i\pi n\theta}}$ describing a situation where the n -th point

has appeared at the origin at time $-n$ in the past. It has then slowly moved outwards on the half-ray $\mathbb{R}_{\geq 0}e^{2i\pi n\theta}$ until reaching its present location $\varphi_\theta(n)$ at the time $t = 0$.

The factor \sqrt{n} in the formula for $\varphi_\theta(n)$ ensures that there are R^2 points (of roughly equal “importance”, measured for example by the area of Voronoi domains) in a disc of large radius R . Areas of Voronoi domains defined by $\varphi_\theta(\mathbb{N})$ are asymptotically equal to π if θ is irrational.

Tools and part of the results of this paper can be adapted to a slightly more general situation given by functions $t \mapsto \rho(t)e^{2i\pi t\alpha(t)}$ where $\rho(t)$ is a suitable increasing function and where the local divergence angle $2\pi\alpha(t)$ is allowed to vary very slowly.

The sequel of the paper is organized as follows:

Section 1 states the main result.

Section 2 recalls a few well-known and useful facts concerning complex lattices and hyperbolic geometry.

Section 3 contains identities involving continuous fraction expansions.

Linearizations of phyllotactic sets are described in Section 4.

We construct the phyllotactic geodesic γ_θ in Section 5. This leads to a proof of Theorem 1.1.

Section 6 describes a construction of a slightly different geodesic.

Section 7 is devoted to metric properties of phyllotactic sets.

Parastichy spirals are defined and studied in Section 8.

Section 9 reviews briefly a few other models appearing in the literature.

Finally, Section 10 discusses a possible experimental verification (or refutation) of the existence of a phyllotactic geodesic in real sunflower-capitula.

1 Main result

Let (E, dist) be a metric space, x an element of E and ϵ, R two strictly positive real numbers. Two discrete subsets A, B of E are ϵ -close in the open ball of radius R and center x if there exists a map $\psi : A' \rightarrow B'$ which is one-to-one and onto between subsets $A' \subset A$ and $B' \subset B$ containing all points in A , respectively B , at distance at most R from x and which moves all points of A' by less than ϵ , i.e., we have $\text{dist}(a, \psi(a)) < \epsilon$ for all $a \in A'$. Intuitively, two discrete sets A, B are ϵ -close in the open ball of radius R centered at x if A and B are “equal up to an error of ϵ ” in (a neighbourhood of) the ball of radius R centered at x .

Theorem 1.1. *Given $\epsilon > 0$ and $R > 0$, there exists an integer $N = N(\epsilon, R)$ such that for every $\theta \in [0, 1)$ and for every $n \geq N$, the set $\varphi_\theta(\mathbb{N})$ is ϵ -close in the open disc of radius R centered at $\varphi_\theta(n)$ to an affine lattice in the equivalence class (i.e. up to orientation-preserving affine similarities) of $\mathbb{Z} + \mathbb{Z}\frac{4i\pi n}{1+4i\pi\{\theta\}n}$.*

The map

$$(0, \infty) \ni t \mapsto \gamma_\theta(t) = \frac{4i\pi t}{1 + 4i\pi\{\theta\}t} = \frac{16\pi^2\{\theta\}t^2 + 4i\pi t}{1 + (4\pi\{\theta\}t)^2}$$

defines a geodesic of the hyperbolic Poincaré halfplane (endowed with the hyperbolic metric $\frac{ds}{y}$ at $z = x + iy \in \mathbb{H}$), see for example Lemma 2.1. We call γ_θ the *phyllotactic geodesic* of φ_θ . Notice that the curve $t \mapsto \gamma_\theta(t)$ has (hyperbolic) speed $\frac{1}{\Im(\gamma_\theta(t))} |\gamma'_\theta(t)| = \frac{1}{t}$ inversely proportional to t .

Remark 1.2. (i) *Theorem 1.1 holds for rational θ : In this case the phyllotactic geodesic ends up in the cusp of the modular curve $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$. The associated affine lattices $\Lambda_{\theta,n}$ degenerate into discrete subgroups of rank 1 in the sense that they intersect a ball of fixed radius R centered at an affine lattice point along a translated copy of a discrete subgroup having rank 1.*

(ii) *Denoting by $V(n)$ the Voronoi domain of $\varphi_\theta(n) \in \varphi_\theta(\mathbb{N})$ we have $\lim_{n \rightarrow \infty} \mathrm{vol}V(n) = \pi$ if θ is irrational.*

For rational $\theta = \frac{p}{q}$ with $q \geq 3$ and p, q coprime integers, the union of Voronoi domains (defined by $\varphi_\theta(\mathbb{N})$) of all points at distance $\leq R$ from the origin is essentially a regular polygon with q sides and inradius R . This implies $\lim_{n \rightarrow \infty} \mathrm{vol}V(n) = q \tan \frac{\pi}{q} = \pi + \frac{\pi^3}{3q^2} + O\left(\frac{1}{q^4}\right)$.

For $\theta \in \frac{1}{2}\mathbb{Z}$, all Voronoi domains are unbounded and thus of infinite volume.

The existence of phyllotactic geodesics gives a measure of “similarity” of phyllotactic sets in neighbourhoods of $\varphi_\theta(n)$ and $\varphi_{\theta'}(m)$ by considering the hyperbolic distance $d_{\mathbb{H}}(\gamma_\theta(n), \mathrm{PSL}_2(\mathbb{Z})\gamma_{\theta'}(m))$ between the two orbits $\mathrm{PSL}_2(\mathbb{Z})\gamma_\theta(n)$ and $\mathrm{PSL}_2(\mathbb{Z})\gamma_{\theta'}(m)$. Statement (ii) of Remark 1.2 ensures that a small distance $d_{\mathbb{H}}(\gamma_\theta(n), \mathrm{PSL}_2(\mathbb{Z})\gamma_{\theta'}(m))$ implies the existence of bijections between $\varphi_\theta(\mathbb{N})$ and $\varphi_{\theta'}(\mathbb{N})$ which are almost isometries in neighbourhoods of $\varphi_\theta(n)$ and $\varphi_{\theta'}(m)$ if θ and θ' are irrational and have continued fraction-expansions with bounded coefficients. More generally, this holds if $\gamma_\theta(n)$ (and thus also $\gamma_{\theta'}(m)$) is far from the cusp of $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$.

2 Complex lattices and hyperbolic geometry

For the convenience of the reader, we recall a few elementary and well-known facts first of the theory of lattices, following closely parts of Section 2.2 in Chapter VII of [11], then of hyperbolic geometry, see for example [1].

2.1 Lattices of \mathbb{C}

A *lattice* in \mathbb{C} is a free additive subgroup generated by two \mathbb{R} -linearly independent elements ω_1, ω_2 of \mathbb{C} . In the sequel, we consider lattices only up to orientation-preserving similarities. Two lattices Γ and Λ of \mathbb{C} are thus

equivalent if $\Lambda = \lambda\Gamma$ for some non-zero constant $\lambda \in \mathbb{C}^*$. Given a basis ω_1, ω_2 of a lattice $\Gamma = \mathbb{Z}\omega_1 + \mathbb{Z}\omega_2$, we consider $z = \frac{\omega_1}{\omega_2}$. Up to replacing, say, ω_1 by $-\omega_1$, we can suppose that the imaginary part $y = \Im(z)$ of $z = x + iy$ is strictly positive.

Thus, a lattice $\mathbb{Z}\omega_1 + \mathbb{Z}\omega_2 = \left(\mathbb{Z} + \mathbb{Z}\frac{\omega_1}{\omega_2}\right)\omega_2$ is equivalent to the lattice $\Gamma(z) = \mathbb{Z} + \mathbb{Z}z$ generated by 1 and by the element $z = \frac{\omega_1}{\omega_2}$ of the open upper half-plane $\mathbb{H} = \{z \in \mathbb{C} \mid \Im(z) > 0\}$.

Given an unimodular integral matrix $g = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \in \mathrm{SL}_2(\mathbb{Z})$, the quotient

$$z' = \frac{\omega'_1}{\omega'_2} = \frac{a\omega_1 + b\omega_2}{c\omega_1 + d\omega_2} = \frac{a\frac{\omega_1}{\omega_2} + b}{c\frac{\omega_1}{\omega_2} + d}$$

associated to the basis $\omega'_1 = a\omega_1 + b\omega_2$, $\omega'_2 = c\omega_1 + d\omega_2$ of a lattice $\mathbb{Z}\omega_1 + \mathbb{Z}\omega_2$ is obtained from $z = \frac{\omega_1}{\omega_2}$ by the usual action $g.z = \frac{az+b}{cz+d}$ of the modular group $\mathrm{PSL}_2(\mathbb{Z}) = \mathrm{SL}_2(\mathbb{Z})/\pm \mathrm{Id}$ on \mathbb{H} .

Hence the map $\mathbb{Z}\omega_1 + \mathbb{Z}\omega_2 \mapsto z = \frac{\omega_1}{\omega_2} \in \mathbb{H}$ induces a one-to-one correspondence between equivalence classes $\mathbb{C}^*\Gamma$ of lattices and points of the modular curve $\mathrm{PSL}_2(\mathbb{Z})\backslash\mathbb{H}$, see Chapter VII, Proposition 2 and Proposition 3 of [11]. A fundamental domain for the action of the modular group $\mathrm{PSL}_2(\mathbb{Z})$ on \mathbb{H} is given by the *fundamental domain*

$$\mathcal{M} = \left\{ z \in \mathbb{C} \mid |z| \geq 1 \text{ and } |\Re(z)| \leq \frac{1}{2} \right\} \quad (1)$$

for $\mathrm{PSL}_2(\mathbb{Z})\backslash\mathbb{H}$. Two elements z_1, z_2 of \mathcal{M} represent the same equivalence-class of lattices if and only if either $z_2 = -\frac{1}{z_1}$ or $z_2 = z_1 \pm 1$. The *modular curve* $\mathrm{PSL}_2(\mathbb{Z})\backslash\mathbb{H} = \mathcal{M}/\sim$ is a complex orbifold with two conical points represented by $\frac{-1+i\sqrt{3}}{2}$ (of angle $\frac{2\pi}{3}$ and corresponding to regular hexagonal lattices) and by i (of angle π and corresponding to square lattices) and with a cusp (corresponding to a neighbourhood of the degenerate case of an additive subgroup of rank 1 in \mathbb{C}).

An *affine lattice* is a coset $\alpha + \Gamma$ obtained by translating a complex lattice $\Gamma \subset \mathbb{C}$ by some vector $\alpha \in \mathbb{C}$. We consider affine lattices only up to orientation-preserving affine similarities. Equivalence classes of affine lattices are also in one-to-one correspondence with elements of the modular curve $\mathrm{PSL}_2(\mathbb{Z})\backslash\mathbb{H}$.

2.2 Hyperbolic geometry on the Poincaré half-plane

We recall a few facts concerning the hyperbolic Poincaré half-plane \mathbb{H} , see [1] for an elementary introduction to hyperbolic geometry.

The upper half-plane $\mathbb{H} = \{z \in \mathbb{C} \mid \Im(z) > 0\}$ can be turned into a real hyperbolic simply connected Riemannian manifold of dimension 2 and of constant curvature -1 by equipping it with the Riemannian metric $(ds)^2 =$

$\frac{dx^2+dy^2}{y^2}$ at a point $z = x + iy \in \mathbb{H}$. The *Poincaré half-plane* is the hyperbolic manifold (still denoted by) \mathbb{H} obtained in this way.

The group of all orientation-preserving isometries of the Poincaré half-plane is given by the set of all Möbius transformations

$$z \mapsto \begin{pmatrix} a & b \\ c & d \end{pmatrix} z = \frac{az + b}{cz + d}$$

defined by matrices $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ in $\mathrm{SL}_2(\mathbb{R})$, representing elements in $\mathrm{PSL}_2(\mathbb{R}) = \mathrm{SL}_2(\mathbb{R}) / \pm \mathrm{Id}$.

The geodesics of \mathbb{H} are half-circles (with respect to the usual Euclidean metric of \mathbb{C}) centered at the boundary \mathbb{R} of $\mathbb{H} \subset \mathbb{C}$ or halflines $\{a + iy \in \mathbb{C} \mid y > 0\} \subset \mathbb{H}$ perpendicular to \mathbb{R} .

An orientation-preserving isometry ι of the Poincaré half-plane is *hyperbolic* if it admits an invariant geodesic on which it acts by a translation. A Möbius transformation associated to $\begin{pmatrix} a & b \\ c & d \end{pmatrix} \in \mathrm{SL}_2(\mathbb{R})$ defines a hyperbolic isometry ι if and only if $|a + d| > 2$. The invariant geodesic of ι is given by the halfcircle in \mathbb{H} delimited by the two real points $\frac{a-d \pm \sqrt{(d-a)^2 + 4bc}}{2c}$ if $c \neq 0$ respectively by the halfline $\{b/(d-a) + iy \mid y > 0\}$ otherwise.

Lemma 2.1. For $\begin{pmatrix} a & b \\ c & d \end{pmatrix} \in \mathrm{GL}_2(\mathbb{R})$ with $cd \neq 0$ and positive determinant $ad - bc > 0$, the image of the map from $\mathbb{R}_{>0} = (0, +\infty)$ into \mathbb{C} defined by

$$t \mapsto \frac{ait + b}{cit + d}$$

is an open half-circle of \mathbb{H} centered on $\frac{ad+bc}{2cd}$ with radius $|\frac{ad-bc}{2cd}|$ (with respect to the Euclidean norm $\|z\| = \sqrt{x^2 + y^2}$ for $z = x + iy \in \mathbb{C}$).

Proof Möbius transformations preserve geodesics of \mathbb{H} . Thus the Möbius transformation defined by the matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ sends the geodesic $\{ti \mid t > 0\} \subset \mathbb{H}$ onto a geodesic of \mathbb{H} with finite boundary points given by $\frac{b}{d}$ (corresponding to $t = 0$) and $\frac{a}{c}$ (corresponding to $t = +\infty$). This geodesic is the open halfcircle (for the usual Euclidean metric of \mathbb{C}) of the upper halfplane with center $\frac{1}{2} \left(\frac{b}{d} + \frac{a}{c} \right) = \frac{ad+bc}{2cd}$ and diameter $|\frac{a}{c} - \frac{ad+bc}{2cd}| = |\frac{ad-bc}{2cd}|$. \square

Remark 2.2. Lemma 2.1 is equivalent to the identity

$$\left(\frac{act^2 + bd}{c^2t^2 + d^2} - \frac{ad + bc}{2cd} \right)^2 + \left(\frac{ad - bc}{c^2t^2 + d^2} \right)^2 t^2 = \left(\frac{ad - bc}{2cd} \right)^2.$$

3 Continued fractions

We denote by $[a_0; a_1, a_2, \dots]$ the continued fraction expansion

$$\theta = a_0 + \frac{1}{a_1 + \frac{1}{a_2 + \ddots}},$$

of a real number θ . The coefficients a_0, a_1, \dots are recursively defined by $a_i = \lfloor \theta_i \rfloor$ where $\theta_0 = \theta$ and $\theta_n = \frac{1}{\theta_{n-1} - a_{n-1}} = \frac{1}{\{\theta_{n-1}\}}$ if $\theta_{n-1} \notin \mathbb{Z}$, respectively by $\theta_n = 0$ if $\theta_{n-1} \in \mathbb{Z}$. The coefficient a_0 of a continued fraction expansion can be an arbitrary integer (positive, zero or negative). a_1, a_2, \dots are either all strictly positive or they start with a finite number of strictly positive integers followed by an infinite string of zeros. The last case arises if and only if θ is rational. The sequence a_0, a_1, \dots is infinite and ultimately periodic with non-zero period if and only if $\mathbb{Q}[\theta]$ is a quadratic number field. Every irrational number has a unique continued fraction expansion. Rational numbers have two expansions given by $[a_0; a_1, \dots, a_m, 1]$ and $[a_0; a_1, \dots, a_m + 1]$ for suitable integers $m \geq 0$, $a_0 \in \mathbb{Z}$, $a_1, \dots, a_m \geq 1$.

We have the continued fraction expansions

$$\theta_n = [a_n; a_{n+1}, a_{n+2}, a_{n+3}, \dots] \quad (2)$$

for all $n \in \mathbb{N}$. *Convergents* for

$$\theta = \theta_0 = a_0 + \frac{1}{a_1 + \frac{1}{a_2 + \ddots}}$$

are rational numbers of the form

$$\frac{p_{-2}}{q_{-2}} = \frac{0}{1}, \frac{p_{-1}}{q_{-1}} = \frac{1}{0}, \frac{p_n}{q_n} = \frac{p_{n-2} + a_n p_{n-1}}{q_{n-2} + a_n q_{n-1}} = [a_0; a_1, \dots, a_n], \quad n \geq 0$$

and can also be define by $\frac{p_n}{q_n} = [a_0; a_1, \dots, a_n]$, see Theorem 149 in [4]. *Intermediate convergents* are given by

$$\frac{p_{n-2} + k p_{n-1}}{q_{n-2} + k q_{n-1}}, \quad k \in \{0, \dots, a_n - 1\}.$$

The easy identity

$$p_{n-1} q_n - p_n q_{n-1} = (-1)^n \quad (3)$$

(see Theorem 150 in [4] or Theorem 2 in [7]), equivalent to $\frac{p_{n-1}}{q_{n-1}} - \frac{p_n}{q_n} = \frac{(-1)^n}{q_{n-1} q_n}$, implies

$$\frac{p_{2n}}{q_{2n}} < \frac{p_{2n+2}}{q_{2n+2}} < \dots < \theta < \dots < \frac{p_{2n+1}}{q_{2n+1}} < \frac{p_{2n-1}}{q_{2n-1}}.$$

This shows

$$\left| \theta - \frac{p_n}{q_n} \right| < \frac{1}{a_{n+1}q_n^2} \quad (4)$$

and ensures that convergents are excellent rational approximations of an irrational number.

The following result is essentially identity 10.3.2 of [4]:

Proposition 3.1. *We have*

$$\theta = \frac{p_{n-2} + \theta_n p_{n-1}}{q_{n-2} + \theta_n q_{n-1}}$$

for all $n \geq 0$.

Proof The result holds for $n = 0$.

We have

$$\begin{aligned} \frac{p_{n-1} + \theta_{n+1} p_n}{q_{n-1} + \theta_{n+1} q_n} &= \frac{p_{n-1} + \frac{1}{\theta_n - a_n} (p_{n-2} + a_n p_{n-1})}{q_{n-1} + \frac{1}{\theta_n - a_n} (q_{n-2} + a_n q_{n-1})} \\ &= \frac{p_{n-2} + \theta_n p_{n-1}}{q_{n-2} + \theta_n q_{n-1}} \end{aligned}$$

which ends the proof by induction. \square

Lemma 3.2. *We have*

$$\frac{\theta_{n+1}}{q_{n-1} + \theta_{n+1} q_n} = \frac{1}{q_{n-2} + \theta_n q_{n-1}} .$$

Proof We have

$$\begin{aligned} \frac{\theta_{n+1}}{q_{n-1} + \theta_{n+1} q_n} &= \frac{1}{\frac{1}{\theta_{n+1}} q_{n-1} + q_n} \\ &= \frac{1}{(\theta_n - a_n) q_{n-1} + q_n} \\ &= \frac{1}{\theta_n q_{n-1} - a_n q_{n-1} + q_{n-2} + a_n q_{n-1}} \end{aligned}$$

where we have used the recursive definitions $\frac{1}{\theta_{n+1}} = \theta_n - a_n$ and $q_n = q_{n-2} + a_n q_{n-1}$ of θ_{n+1} and of q_n . \square

Proposition 3.3. *We have*

$$\theta - \frac{p_{n-2} + x p_{n-1}}{q_{n-2} + x q_{n-1}} = \frac{(\theta_n - x)(-1)^n}{(q_{n-2} + x q_{n-1})(q_{n-2} + \theta_n q_{n-1})} . \quad (5)$$

Proof Proposition 3.1 shows that the result holds for $x = \theta_n$.

Since (5) is equivalent to the identity

$$(q_{n-2} + xq_{n-1})\theta - (p_{n-2} + xp_{n-1}) = \frac{\theta_n - x}{q_{n-2} + \theta_n q_{n-1}} (-1)^n \quad (6)$$

involving affine functions of x , it is enough to show the equality

$$q_{n-1}\theta - p_{n-1} = -\frac{(-1)^n}{q_{n-2} + \theta_n q_{n-1}}. \quad (7)$$

This holds for $n = 0$ since it boils down to $-1 = -1$. By induction, we have for $x = a_n$ the identity

$$\theta - \frac{p_{n-2} + a_n p_{n-1}}{q_{n-2} + a_n q_{n-1}} = \frac{(\theta_n - a_n)(-1)^n}{(q_{n-2} + a_n q_{n-1})(q_{n-2} + \theta_n q_{n-1})}$$

which can be rewritten as

$$\theta - \frac{p_n}{q_n} = \frac{(-1)^n}{\theta_{n+1} q_n (q_{n-2} + \theta_n q_{n-1})} \quad (8)$$

using the recursive definitions of p_n , q_n and θ_{n+1} .

The identity

$$\theta_{n+1} (q_{n-2} + \theta_n q_{n-1}) = q_{n-1} + \theta_{n+1} q_n$$

equivalent to Lemma 3.2 yields now (7) for $n + 1$. \square

Remark 3.4. Identity (8) (corresponding to the specialization $x = a_n$ of Proposition 3.3) strengthens inequality (4) since $a_{n+1} = \lfloor \theta_{n+1} \rfloor \leq \theta_{n+1}$ and $q_n = q_{n-2} + a_n q_{n-1} \leq q_{n-2} + \theta_n q_{n-1}$.

Lemma 3.5. We have

$$\frac{1}{q_{n-2} + \theta_n q_{n-1}} - \frac{a_{n+1}}{q_{n-1} + \theta_{n+1} q_n} = \frac{1}{q_n + \theta_{n+2} q_{n+1}}.$$

Proof Using the identities

$$\begin{aligned} q_k &= q_{k-2} + a_k q_{k-1}, \\ \theta_{k+1} &= \frac{1}{\theta_k - a_k}, \end{aligned}$$

for $k = n$ and $k = n + 1$ we have

$$\begin{aligned}
& \frac{1}{q_{n-2} + \theta_n q_{n-1}} - \frac{a_{n+1}}{q_{n-1} + \theta_{n+1} q_n} \\
&= \frac{1}{q_n - a_n q_{n-1} + \theta_n q_{n-1}} - \frac{a_{n+1}}{q_{n-1} + \theta_{n+1} q_n} \\
&= \frac{1}{q_n + \frac{1}{\theta_{n+1}} q_{n-1}} - \frac{a_{n+1}}{q_{n-1} + \theta_{n+1} q_n} \\
&= \frac{\theta_{n+1} - a_{n+1}}{q_{n-1} + \theta_{n+1} q_n} \\
&= \frac{\theta_{n+1} - a_{n+1}}{q_{n-1} + a_{n+1} q_n + (\theta_{n+1} - a_{n+1}) q_n} \\
&= \frac{1}{\theta_{n+2} q_{n+1} + q_n}
\end{aligned}$$

which ends the proof. \square

4 Linearization

Proposition 4.1. *We have*

$$\begin{aligned}
\varphi_\theta(n + a q_{j-1} + b q_j) - \varphi_\theta(n) &= a \left(\frac{q_{j-1}}{2\sqrt{n}} - \frac{(-1)^j 2i\pi \sqrt{n} \theta_{j+1}}{q_{j-1} + \theta_{j+1} q_j} \right) e^{2i\pi n \theta} \\
&+ b \left(\frac{q_j}{2\sqrt{n}} + \frac{(-1)^j 2i\pi \sqrt{n} \theta_{j+2}}{q_j + \theta_{j+2} q_{j+1}} \right) e^{2i\pi n \theta} \\
&+ E_j(a, b)
\end{aligned}$$

where q_k is the denominator of the k -th convergent $\frac{p_k}{q_k} = [a_0; a_1, \dots, a_k]$ for $\theta = [a_0; a_1, a_2, \dots]$, where $\theta_k = [a_k; a_{k+1}, a_{k+2}, \dots]$ is defined as in (2) and where the error $E_j(a, b)$ is asymptotically given by

$$\left(\frac{-1}{8n^{3/2}} (a q_{j-1} + b q_j)^2 + \frac{i\pi}{\sqrt{n}} (a q_{j-1} + b q_j) \delta - 2\pi^2 \sqrt{n} \delta^2 \right) e^{2i\pi n \theta}$$

with

$$\delta = -a \frac{(-1)^j \theta_{j+1}}{q_{j-1} + \theta_{j+1} q_j} + b \frac{(-1)^j \theta_{j+2}}{q_j + \theta_{j+2} q_{j+1}}$$

if $|\varphi_\theta(n + a q_{j-1} + b q_j) - \varphi_\theta(n)| = O(1)$.

Corollary 4.2. *If q_{j-1} and q_j are denominators of two consecutive convergents $\frac{p_{j-1}}{q_{j-1}}$ and $\frac{p_j}{q_j}$ of θ such that $q_{j-1} \leq \sqrt{n} < q_j$, then the smallest points of*

$$(\varphi_\theta(\mathbb{N}) - \varphi_\theta(n)) e^{-2i\pi n \theta}$$

are close to the smallest points of the lattice

$$\mathbb{Z} \left(\frac{q_{j-1}}{2\sqrt{n}} - (-1)^j \frac{2i\pi\sqrt{n}\theta_{j+1}}{q_{j-1} + \theta_{j+1}q_j} \right) + \mathbb{Z} \left(\frac{q_j}{2\sqrt{n}} + (-1)^j \frac{2i\pi\sqrt{n}\theta_{j+2}}{q_j + \theta_{j+2}q_{j+1}} \right) \quad (9)$$

with an error of order $O\left(\frac{1}{\sqrt{n}}\right)$.

The lattice described by (9) contains always a non-zero element of absolute value smaller than $\sqrt{\frac{1}{4} + 4\pi^2} < 3\pi$.

Remark 4.3. *Fundamental domains of the lattice Λ given by (9) have area π as shown by the identities*

$$\begin{aligned} & (-1)^j \det \begin{pmatrix} \frac{q_{j-1}}{2\sqrt{n}} & -\frac{(-1)^j 2i\pi\sqrt{n}\theta_{j+1}}{q_{j-1} + \theta_{j+1}q_j} \\ \frac{q_j}{2\sqrt{n}} & +\frac{(-1)^j 2i\pi\sqrt{n}\theta_{j+2}}{q_j + \theta_{j+2}q_{j+1}} \end{pmatrix} \\ &= \left(q_{j-1} \frac{\theta_{j+2}}{q_j + \theta_{j+2}q_{j+1}} + q_j \frac{\theta_{j+1}}{q_{j-1} + \theta_{j+1}q_j} \right) \pi \\ &= \left(q_{j-1} \frac{1}{q_{j-1} + \theta_{j+1}q_j} + q_j \frac{\theta_{j+1}}{q_{j-1} + \theta_{j+1}q_j} \right) \pi \\ &= \pi \end{aligned}$$

where the second equality is given by Lemma 3.2.

Since the regular hexagonal lattice has maximal density, the lattice Λ contains always a non-zero element of absolute value at most $\sqrt{\frac{2\pi}{\sqrt{3}}} \sim 1.9046$.

Proof of Proposition 4.1 Setting

$$F(s, \gamma) = \sqrt{n+s} e^{2i\pi n\theta + 2i\pi\gamma}$$

we want to approximate

$$F(aq_{j-1} + bq_j, \delta) - F(0, 0)$$

where $\delta = (aq_{j-1} + bq_j)\theta - c$ is the difference between $(aq_{j-1} + bq_j)\theta$ and the integer c closest to $(aq_{j-1} + bq_j)\theta$. We do this in the usual way by considering the linear approximation

$$L = \frac{\partial F}{\partial s}(0, 0)(aq_{j-1} + bq_j) + \frac{\partial F}{\partial \gamma}(0, 0)\delta$$

and by estimating the error using second-order derivatives. The necessary

partial derivatives of F are:

$$\begin{aligned}\frac{\partial F}{\partial s}(0,0) &= \frac{1}{2\sqrt{n}}e^{2i\pi n\theta}, \\ \frac{\partial F}{\partial \gamma}(0,0) &= 2i\pi\sqrt{n}e^{2i\pi n\theta}, \\ \frac{\partial^2 F}{\partial s^2}(0,0) &= \frac{-1}{4n^{3/2}}e^{2i\pi n\theta}, \\ \frac{\partial^2 F}{\partial s\partial \gamma}(0,0) &= \frac{i\pi}{\sqrt{n}}e^{2i\pi n\theta}, \\ \frac{\partial^2 F}{\partial \gamma^2}(0,0) &= -4\pi^2\sqrt{n}e^{2i\pi n\theta}.\end{aligned}$$

The contribution coming from $\frac{\partial F}{\partial s}(0,0)(aq_{j-1} + bq_j)$ to L is given by

$$\frac{1}{2\sqrt{n}}e^{2i\pi n\theta}(aq_{j-1} + bq_j).$$

In order to compute $\frac{\partial F}{\partial \gamma}(0,0)\delta$ we split δ into $\delta = a\delta_{j-1} + b\delta_j$ where δ_k for $k \in \{j-1, j\}$ is the difference between $q_k\theta$ and the integer closest to $q_k\theta$. Since q_k is a denominator of the convergent $\frac{p_k}{q_k} = [a_0; a_1, \dots, a_k]$ of θ , this integer is given by the numerator p_k . We have

$$\begin{aligned}\theta - \frac{p_k}{q_k} &= \frac{p_k + \theta_{k+2}p_{k+1}}{q_k + \theta_{k+2}q_{k+1}} - \frac{p_k}{q_k} \\ &= \frac{(p_{k+1}q_k - p_kq_{k+1})\theta_{k+2}}{q_k(q_k + \theta_{k+2}q_{k+1})} \\ &= (-1)^k \frac{\theta_{k+2}}{q_k(q_k + \theta_{k+2}q_{k+1})}\end{aligned}$$

where we have used Proposition 3.1 and identity (3). This yields

$$\delta_k = (-1)^k \frac{\theta_{k+2}}{q_k + \theta_{k+2}q_{k+1}}$$

and shows

$$\begin{aligned}\frac{\partial F}{\partial s}(0,0)\delta &= \frac{\partial F}{\partial s}(0,0)(a\delta_{j-1} + b\delta_j) \\ &= \frac{\partial F}{\partial s}(0,0) \left(-a \frac{(-1)^j \theta_{j+1}}{q_{j-1} + \theta_{j+1}q_j} + b \frac{(-1)^j \theta_{j+2}}{q_j + \theta_{j+2}q_{j+1}} \right).\end{aligned}$$

The order of the error is given by

$$\frac{1}{2} \frac{\partial^2 F}{\partial s^2}(0,0)(aq_{j-1} + bq_j)^2 + \frac{\partial^2 F}{\partial s\partial \gamma}(0,0)(aq_{j-1} + bq_j)\delta + \frac{1}{2} \frac{\partial^2 F}{\partial \gamma^2}(0,0)\delta^2$$

and can be evaluated easily. \square

5 The phyllotactic geodesic and proof of Theorem 1.1

Using (3.2) we can rewrite the lattice Λ given by formula (9) of Corollary 4.2 as

$$\mathbb{Z} \left(\frac{q_{j-1}}{2\sqrt{n}} - (-1)^j \frac{2i\pi\sqrt{n}}{q_{j-2} + \theta_j q_{j-1}} \right) + \mathbb{Z} \left(\frac{q_j}{2\sqrt{n}} + (-1)^j \frac{2i\pi\sqrt{n}}{q_{j-1} + \theta_{j+1} q_j} \right).$$

In particular, the lattice Λ is similar to the lattice $\mathbb{Z} + \mathbb{Z}\tau_j(n)$ where

$$\tau_j(t) = -(-1)^j \frac{q_{j-1} - (-1)^j \frac{4i\pi t}{q_{j-2} + \theta_j q_{j-1}}}{q_j + (-1)^j \frac{4i\pi t}{q_{j-1} + \theta_{j+1} q_j}}. \quad (10)$$

Remark 5.1. *A straightforward computation shows that the imaginary part of $\tau_j(t)$, given by*

$$\frac{\frac{q_{j-1}}{q_{j-1} + \theta_{j+1} q_j} + \frac{q_j}{q_{j-2} + \theta_j q_{j-1}}}{q_j^2 + \frac{16\pi^2 t^2}{(q_{j-1} + \theta_{j+1} q_j)^2}} 4\pi t,$$

is strictly positive if t is strictly positive.

Theorem 5.2. *For all $j \geq 0$ we have*

$$(\tau_j(t) - (-1)^j a_{j+1}) \tau_{j+1}(t) = -1.$$

Proof Theorem 5.2 boils down to the identity

$$\begin{aligned} & q_{j-1} - (-1)^j \frac{4i\pi t}{q_{j-2} + \theta_j q_{j-1}} + a_{j+1} q_j + a_{j+1} (-1)^j \frac{4i\pi t}{q_{j-1} + \theta_{j+1} q_j} \\ &= q_{j+1} - (-1)^j \frac{4i\pi t}{q_j + \theta_{j+2} q_{j+1}}. \end{aligned}$$

The identity $q_{j+1} = q_{j-1} + a_{j+1} q_j$ shows that the constant parts (with respect to t) of both sides are equal. Linear coefficients of t are equal by Lemma 3.5. \square

Proof of Theorem 1.1 By Theorem 5.2, the two geodesics defined by τ_j and τ_{j+1} are related by the integral Möbius transformations

$$\tau_{j+1} = \frac{-1}{\tau_j - (-1)^j a_{j+1}} = \begin{pmatrix} 0 & 1 \\ -1 & (-1)^j a_{j+1} \end{pmatrix} \cdot \tau_j \quad (11)$$

and

$$\tau_j = \frac{(-1)^j a_{j+1} \tau_{j+1} - 1}{\tau_{j+1}} = \begin{pmatrix} (-1)^j a_{j+1} & -1 \\ 1 & 0 \end{pmatrix} \cdot \tau_{j+1}. \quad (12)$$

Thus they project onto a unique geodesic on the modular curve $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$ represented for example by

$$\tau_0(t) = -\frac{q_{-1} - \frac{4i\pi t}{q_{-2} + \theta_0 q_{-1}}}{q_0 + \frac{4i\pi t}{q_{-1} + \theta_1 q_0}} = \frac{4i\pi t}{1 + \frac{4i\pi t}{\theta_1}} = \frac{4i\pi t}{1 + 4i\pi\{\theta\}t} \quad (13)$$

(where $q_{-2} = 1$, $q_{-1} = 0$, $q_0 = 1$ and $\theta_1 = \frac{1}{\theta - a_0} = \frac{1}{\{\theta\}}$).

This implies Theorem 1.1 since the linearization error is of order $O\left(\frac{1}{\sqrt{n}}\right)$ for elements of $\varphi_\theta(\mathbb{N})$ at bounded distance from $\varphi_\theta(n)$. \square

Formula (13) defines a geodesic of the hyperbolic half-plane for every real number θ . Indeed, (13) is a vertical half-line (and thus a geodesic) if θ is integral and it defines a halfcircle of \mathbb{H} orthogonal to \mathbb{R} (and thus a geodesic) with boundary points 0 corresponding to $t = 0$ and $\frac{1}{\{\theta\}}$ corresponding to $t = \infty$ otherwise.

Diophantine properties of θ are related to the dynamical behaviour of the geodesic γ_θ projected onto $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$ as follows: after starting at the cusp, (the projection of) γ_θ turns (slightly less) than a_1 times around the cusp before passing between the two conical points of the modular curve. It turns then in the same sense (and slightly less than) a_2 times around the cusp before crossing again the shortest geodesic segment joining the two conical points and so on. A large coefficient a_k causes the (projection of the) geodesic γ_θ to climb the modular curve up to a height given asymptotically (in a_k) by $a_k i \in \mathcal{M}$. This gives rise to points of $\varphi_\theta(\mathbb{N})$ having Voronoi domains with bad isoperimetric properties.

For a divergence angle $2\pi\theta$ determined by the golden ratio $\theta = \frac{1+\sqrt{5}}{2}$ (or close relatives of it) the continued fraction expansion involves only ones (or only ones after perhaps a few initial ‘‘accidents’’). This is the optimal situation leaving no possibility of improvement. In particular, the phyllotactic geodesic $\gamma_{(1+\sqrt{5})/2}$ is asymptotically equal to the geodesic

$$t \mapsto \tilde{\gamma}(t) = \frac{(-1 + \sqrt{5})it - 1 - \sqrt{5}}{2(it + 1)} = \frac{-1 - \sqrt{5} + (-1 + \sqrt{5})t^2 + 2it\sqrt{5}}{2(1 + t^2)}$$

with boundary points $\frac{-1 \pm \sqrt{5}}{2}$ (and containing the points $-1 + i = \tilde{\gamma}\left(\frac{-1 + \sqrt{5}}{2}\right)$ and $i = \tilde{\gamma}\left(\frac{1 + \sqrt{5}}{2}\right)$ of \mathbb{H}). The equality

$$\tilde{\gamma}(\theta^4 t) = \frac{\tilde{\gamma}(t) + 1}{\tilde{\gamma}(t) + 2}$$

shows that $\tilde{\gamma}$ is invariant under the integral Möbius transformation defined by the matrix $\begin{pmatrix} 1 & 1 \\ 1 & 2 \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ 1 & 1 \end{pmatrix}^2$. It projects onto the shortest closed geodesic of the modular curve $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$.

Since $\frac{d}{dt}\tilde{\gamma}(t) = \frac{-\sqrt{5}}{(t-i)^2}$, the parametrized geodesic $\tilde{\gamma}(t)$ has the same instant speed $\frac{1}{\Im(\tilde{\gamma}(t))}|\tilde{\gamma}'(t)| = \frac{1}{t}$ as the phyllotactic geodesic $\gamma_\theta(t)$. We have thus asymptotically $\gamma_\theta(t) \sim \gamma_\theta(\theta^4 t)$. The phyllotactic set $\varphi_\theta(\mathbb{N})$ has thus almost isometrical neighbourhoods around $\varphi_\theta(n)$ and $\varphi_\theta(m)$ if n is large and m is close to $\theta^4 n$.

6 A geometric construction

We construct in this section a slightly different geodesic on the modular domain $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$ which is asymptotically associated to linearizations of $\varphi_\theta(\mathbb{N})$.

We denote by $\mathcal{L} = \mathcal{L}_\theta$ the line $\mathbb{R}(1, -\theta)$ of slope $-\theta$ containing the origin. A convergent $\frac{p_j}{q_j} = [a_0; a_1, \dots, a_j]$ of $\theta = [a_0; a_1, a_2, \dots]$ yields an integral point $(q_j, -p_j)$ close to \mathcal{L} as follows: Denoting by $\pi_{\mathcal{L}}(q_j, -p_j)$ the orthogonal projection of $(q_j, -p_j)$ onto \mathcal{L} we have

$$\pi_{\mathcal{L}}(q_j, -p_j) = q_j(1, -\theta) + O\left(\frac{1}{q_j}\right)(1, -\theta)$$

for all $j \geq 0$. The equality $q_j\theta - p_j = (-1)^j \frac{\theta_{j+2}}{q_j + \theta_{j+2}q_{j+1}}$ corresponding to the case $n = j + 2$ and $x = 0$ of Proposition 3.3 implies the identity

$$(q_j, -p_j) - q_j(1, -\theta) = \left(0, (-1)^j \frac{\theta_{j+2}}{q_j + \theta_{j+2}q_{j+1}}\right).$$

The orthogonal projection $\pi_{\mathcal{L}^\perp}(q_j, -p_j)$ of $(q_j, -p_j)$ onto the line $\mathcal{L}^\perp = \mathbb{R}(\theta, 1)$ orthogonal to $\mathcal{L} = \mathbb{R}(1, -\theta)$ is given by

$$\begin{aligned} \pi_{\mathcal{L}^\perp}(q_j, -p_j) &= \pi_{\mathcal{L}^\perp}((q_j, -p_j) - q_j(1, -\theta)) \\ &= \frac{(-1)^j \theta_{j+2}}{(q_j + \theta_{j+2}q_{j+1})} \frac{(\theta, 1)}{(1 + \theta^2)}. \end{aligned}$$

Thus we can rewrite the right side of the obvious identity

$$(q_j, -p_j) = \pi_{\mathcal{L}}(q_j, -p_j) + \pi_{\mathcal{L}^\perp}(q_j, -p_j)$$

as

$$q_j(1, -\theta) + \frac{(-1)^j 4\pi n \theta_{j+2}}{(q_j + \theta_{j+2}q_{j+1})} \frac{(\theta, 1)}{4\pi n(1 + \theta^2)} + O\left(\frac{1}{q_j}\right)(1, -\theta). \quad (14)$$

We endow now \mathbb{R}^2 with an Euclidean metric $ds_{\theta, n}$ turning the vectors $(1, -\theta), \frac{(\theta, 1)}{4\pi n(1 + \theta^2)}$ into an orthogonal basis. Comparison of (14) with (9)

shows that the lattice $(\mathbb{Z}^2, ds_{\theta,n})$ is asymptotically equivalent with the linearization of $\varphi_\theta(\mathbb{N})$ at the point $\varphi_\theta(n)$. Since

$$\begin{aligned}(1, 0) &= \frac{1}{1+\theta^2}(1, -\theta) + 4\pi n\theta \frac{(\theta, 1)}{4\pi n(1+\theta^2)}, \\ (0, 1) &= -\frac{\theta}{1+\theta^2}(1, -\theta) + 4\pi n \frac{(\theta, 1)}{4\pi n(1+\theta^2)},\end{aligned}$$

the Euclidean lattice $(\mathbb{Z}^2, ds_{\theta,n})$ corresponds to the point of $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$ represented by

$$\begin{aligned}& \frac{1 + 4i\pi n\theta(1 + \theta^2)}{\theta - 4i\pi n(1 + \theta^2)} \\ &= \frac{\theta - 16\pi^2 n^2 \theta(1 + \theta^2)^2 + 4i\pi n(1 + \theta^2)^2}{\theta^2 + 16\pi^2 n^2(1 + \theta^2)^2}.\end{aligned}$$

All these points are elements of the hyperbolic geodesic with boundary points $\frac{1}{\theta}$ (for $n = 0$) and $-\theta = \begin{pmatrix} a_0 & 1 \\ -1 & 0 \end{pmatrix} \frac{1}{\{\theta\}}$ (for $n = \infty$).

Remark 6.1. *Since we have*

$$\begin{aligned}& \frac{1 + 4i\pi t\theta(1 + \theta^2)}{\theta - 4i\pi t(1 + \theta^2)} - \begin{pmatrix} a_0 & 1 \\ -1 & 0 \end{pmatrix} \frac{4i\pi t}{4i\pi\{\theta\}t + 1} \\ &= \frac{1 + 4i\pi t\theta(1 + \theta^2)}{\theta - 4i\pi t(1 + \theta^2)} + \frac{4i\pi\theta t + 1}{4i\pi t} \\ &= \frac{\theta}{4i\pi t(\theta - 4i\pi t(1 + \theta^2))} \\ &= \frac{1 + \theta^2}{\theta^2 + 16\pi^2 t^2(1 + \theta^2)^2} - \frac{\theta^2}{4\pi t(\theta^2 + 16\pi^2 t^2(1 + \theta^2)^2)}i,\end{aligned}$$

the hyperbolic distance between the two points

$$\frac{1 + 4i\pi t\theta(1 + \theta^2)}{\theta - 4i\pi t(1 + \theta^2)} \text{ and } \begin{pmatrix} a_0 & 1 \\ -1 & 0 \end{pmatrix} \frac{4i\pi t}{4i\pi\{\theta\}t + 1}$$

of \mathbb{H} is roughly given by

$$\left| \frac{\theta^2 + 16\pi^2 t^2(1 + \theta^2)^2}{4\pi t(1 + \theta^2)^2} \left| \frac{1 + \theta^2}{\theta^2 + 16\pi^2 t^2(1 + \theta^2)^2} - \frac{\theta^2}{4\pi t(\theta^2 + 16\pi^2 t^2(1 + \theta^2)^2)}i \right| \right|$$

which simplifies to

$$\left| \frac{1}{4\pi t(1 + \theta^2)} - \frac{\theta^2}{16\pi^2 t^2}i \right|.$$

Thus it is asymptotically equal to $\frac{1}{4\pi t(1+\theta^2)}$ which is asymptotically much smaller than the error $O\left(\frac{1}{\sqrt{n}}\right)$ due to linearization at a point $\varphi_\theta(n) = \sqrt{n}e^{2i\pi\theta n}$ of order $O(\sqrt{t})$.

7 Metric properties of phyllotactic sets

A subset S of a metric space E is *uniformly discrete* if there exists a strictly positive real constant δ such that $d(a, b) \geq \delta$ for every pair a, b of distinct points in S . Equivalently, S is uniformly discrete if open balls of radius $\delta/2$ centered at all elements of E are disjoint (for a small strictly positive constant δ).

A subset \mathcal{S} of a metric space E is an ϵ -*net* if every point of E is at distance at most ϵ from a point of \mathcal{S} . Equivalently, E is covered by the set of closed balls of radius ϵ centered at elements of \mathcal{S} .

The following result is a straightforward consequence of the fact that areas of Voronoi domains defined by $\varphi_\theta(\mathbb{N})$ are asymptotically equal to π if θ is irrational:

Proposition 7.1. *The following assertions are equivalent:*

(i) θ is irrational and has bounded coefficients a_1, a_2, \dots in its continued fraction expansion $\theta = [a_0; a_1, a_2, \dots]$.

(ii) $\varphi_\theta(\mathbb{N})$ is uniformly discrete in \mathbb{C} (identified with the Euclidean plane in the obvious way).

(iii) $\varphi_\theta(\mathbb{N})$ is an ϵ -net of \mathbb{C} .

(iv) All Voronoi domains of $\varphi_\theta(\mathbb{N})$ have bounded diameter.

(v) Discs of radius R (and arbitrary centers) in \mathbb{C} contain $R(R + O(1))$ points of $\varphi_\theta(\mathbb{N})$.

(vi) The image $\gamma_\theta([1, \infty))$ of the phyllotactic “half-geodesic” is contained in a compact subset of the modular curve $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$.

We leave the proof to the reader. □

Observe that $\varphi_\theta(\mathbb{N})$ is never uniformly discrete if θ is rational.

8 Parastichy spirals

We denote by $\partial\mathcal{M}$ the boundary in \mathbb{C} of the fundamental domain \mathcal{M} defined by (1). The interior $\mathcal{M} \setminus \partial\mathcal{M}$ corresponds to lattices having a unique pair $\pm u$ of opposite shortest non-zero vectors and a unique pair $\pm v$ of shortest vectors which are \mathbb{R} -linearly independent from $\pm u$. More precisely, for $z \in \mathcal{M} \setminus \partial\mathcal{M}$ the unique pair $\pm u$ of non-zero shortest vectors in $\mathbb{Z} + \mathbb{Z}z$ is given by ± 1 and the unique pair $\pm v$ of shortest vectors outside \mathbb{R} coincides with $\pm z$. Notice that \mathbb{R} -linear independency of v from u is necessary in order to discard $\pm 2u, \pm 3u, \dots$ which might be smaller than v for lattices associated to $z \in \mathcal{M}$ with large modulus.

Lattices corresponding to elements z of norm 1 in \mathcal{M} have (at least) two pairs of shortest vectors given by ± 1 and $\pm z$ in $\mathbb{Z} + \mathbb{Z}z$. The regular hexagonal lattice corresponding to $z = \frac{1+i\sqrt{3}}{2}$ is the unique lattice with three pairs $\pm 1, \pm \frac{1+i\sqrt{3}}{2}, \pm \frac{1-i\sqrt{3}}{2}$ of shortest non-zero vectors. Lattices associated

to $z = \frac{1+it}{2}$ for $t > \sqrt{3}$ have a unique pair ± 1 of shortest non-zero-vectors and two non-real pairs $\pm z$ and $\pm(z-1)$ of shortest non-real vectors.

Connecting points of a lattice Λ indexed by $z \in \mathcal{M} \setminus \partial\mathcal{M}$ with their closest neighbours we get a set of parallel lines. Joining closest lattice-points on two such adjacent lines we obtain a second set of parallel lines. These two sets of parallel lines cut the complex plane into fundamental domains for Λ given by isometric rhombi.

Parastichy spirals are analogues of these lines in $\varphi_\theta(\mathbb{N})$. More precisely, we define (generically) the *primary parastichy spirals* of $\varphi_\theta(\mathbb{N})$ as the piecewise-wise linear paths obtained by joining vertices of $\varphi_\theta(\mathbb{N})$ to their two approximatively opposite nearest neighbours. Similarly, we construct *secondary parastichy spirals* by joining vertices of $\varphi_\theta(\mathbb{N})$ to their nearest neighbours on adjacent neighbouring primary parastichy spirals.

Primary parastichy spirals exist essentially at every point far from the origin except where they become blurred with secondary parastichy spirals. At such points (corresponding to crossings of the phyllotactic geodesic with the image of the unit circle in $\mathrm{PSL}_2(\mathbb{Z}) \setminus \mathbb{H}$), primary and secondary parastichy spirals get exchanged. We call such a situation a *parastichy transition of type I*.

Secondary parastichy spirals are however well-defined only if the local situation corresponds to a lattice indexed by an element of \mathcal{M} which is not too close to the cusp. For example, the phyllotactic set $\varphi_\theta(\mathbb{N})$ associated to a rational number $\theta = \frac{p}{q}$ is contained in q half-rays originating at 0. Far from the origin, primary parastichies (and are no longer spirals) coincide with these half-rays and secondary parastichies make no longer sense. Moreover, for points $z \in \mathcal{M}$ with real part close to $1/2$ (or $-1/2$) a family of secondary parastichy spirals fades away and is replaced by a new family of secondary parastichy spirals, giving rise to a *parastichy transition of type II*. A coefficient $a_i > 1$ yields $a_i - 1$ parastichy transitions of type II. The occurrence of parastichy transitions of type II is easy to detect visually: it leads to much less uniform point distributions in $\varphi_\theta(\mathbb{N})$. Figure 4 displays two examples.

The geometric construction of Section 6 shows the well-known fact that primary and secondary parastichies form two sets of spirals with different orientations if θ is irrational. Indeed, primary, respectively secondary, parastichies around $\varphi_\theta(n)$ are defined by $\varphi_\theta(n \pm q_j)$, respectively by $\varphi_\theta(n \pm (q_{j-1} + kq_j))$ for suitable integers j, k , see Figure 2 where one has to think of $(0, 0)$ as the point $\varphi_\theta(n)$ and of \mathcal{L} as the ray defined by $\mathbb{R}_{>0}\varphi_\theta(n)$. (As always, q_{j-1} and q_j are denominators of convergents for θ .) The same integers j, k work for all n in some interval of large length compared to \sqrt{n} . The plane \mathbb{R}^2 is increasingly squeezed (for increasing n) in the direction of \mathcal{L} and expanded in the orthogonal direction \mathcal{L}^\perp in the construction of Section 6. This implies that parastichies of both kinds bend away from the rays issued by the origin. Moreover, there is exactly one parastichy family of larger, respectively of smaller slope than $\varphi_\theta(n)$ as can be seen by inspecting Figure

2. This explains the apparition of crisscrossing spirals in Figure 1. Secondary parastichy families are however no longer discernible (to the eye) for larger values of k , see Figure 4 where there are regions without obvious secondary parastichies. For irrational θ , they can however always be drawn “by continuity”, if we start in suitable regions where no problems occur and if we push them forward using type II transition for (the projection of) γ_θ crossing the infinite boundary segment of \mathcal{M} .

8.1 Transitions for parastichy families

The number of “parallel” primary parastichy spirals forming a common family is always a denominator q_j of a convergent $\frac{p_j}{q_j} = [a_0; a_1, \dots, a_j]$ of the divergence angle $2\pi\theta = 2\pi[a_0, a_1, a_2, \dots]$. The number of secondary parastichy spirals in a common family is a denominator $q_j + kq_{j+1}$, $k \in \{0, 1, \dots, a_{j+2}\}$ of an intermediate convergent.

The exterior region of Figure 1 for example contains 55 primary parastichy spirals turning clockwise and 34 secondary parastichy spirals turning counterclockwise.

The evolution of the numbers of parastichy spirals (PS in the following table) can be described by:

	\vdots	\vdots	\vdots
I	q_{j-1} prim. PS	$ \overline{\gamma_\theta(n)} \sim 1$	q_j sec. PS
	q_{j-1} sec. PS		q_j prim. PS
II	$q_{j-1} + q_j$ sec. PS	$ \Re(\overline{\gamma_\theta(n)}) \sim \frac{1}{2}$	q_j prim. PS
II	$q_{j-1} + 2q_j$ sec. PS	$ \Re(\overline{\gamma_\theta(n)}) \sim \frac{1}{2}$	q_j prim. PS
II	\vdots	\vdots	\vdots
I	$q_{j-1} + a_{j+1}q_j = q_{j+1}$ sec. PS	$ \overline{\gamma_\theta(n)} \sim 1$	q_j prim. PS
	q_{j+1} prim. PS		q_j sec. PS
II	q_{j+1} prim. PS	$ \Re(\overline{\gamma_\theta(n)}) \sim \frac{1}{2}$	$q_j + q_{j+1}$ sec. PS
	\vdots	\vdots	\vdots

where $\overline{\gamma_\theta(n)}$ denotes a representant of $\gamma_\theta(n)$ in \mathcal{M} .

Figure 2 attempts to illustrate the occurrence of parastichy transitions using the geometric construction.

Figure 3 shows the death and birth of a family of secondary parastichy spirals corresponding to a value of n such that $|\Re(\overline{\gamma_\theta(n)})| \sim \frac{1}{2}$. The vertical arrow represents a ray issued from the origin. Primary parastichies are represented by fat segments, the dying family of secondary parastichies is drawn with dotted segments and the newborn family of secondary parastichies is given by ordinary segments. Turning around the origin on a circle

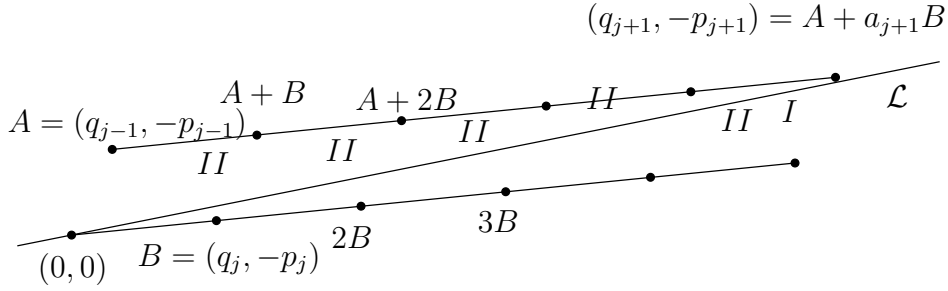


Figure 2: Parastichy transitions

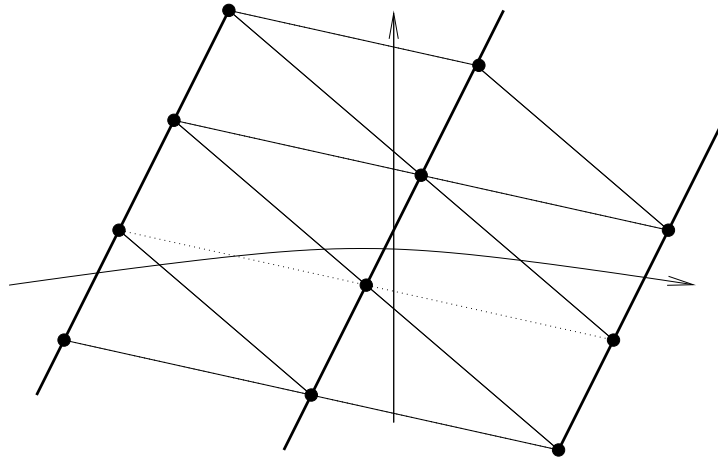


Figure 3: Death and birth of a family of secondary parastichy spirals

of constant radius $\sim \sqrt{n}$ and counting the numbers a of primary parastichy spirals, b of dying secondary parastichies and c of newborn secondary parastichies, one gets the relation $c = a + b$. More precisely, the piecewise linear path involving only segments of primary and secondary dying parastichies giving the best approximation of the circle with radius \sqrt{n} consists of b segments on primary parastichies and a segments on secondary parastichies. In order to work with the family of newborn parastichies, one has to replace every segment of the dying family by two segments, one from a primary parastichy and one from a newborn secondary parastichy. The number of segments on secondary parastichies (which is equal to the number of curves in the primary family) remains thus constant (and equals a) and the number c of segments on primary parastichies (which equals the number c of curves in the newborn secondary parastichy family) increases by a to $c = a + b$.

In order to prove that parastichy families are enumerated by denominators of (intermediate) convergents, it is now enough to remark that the assertion holds for the final number of primary parastichies if θ is rational. A continuity argument implies the result in general.

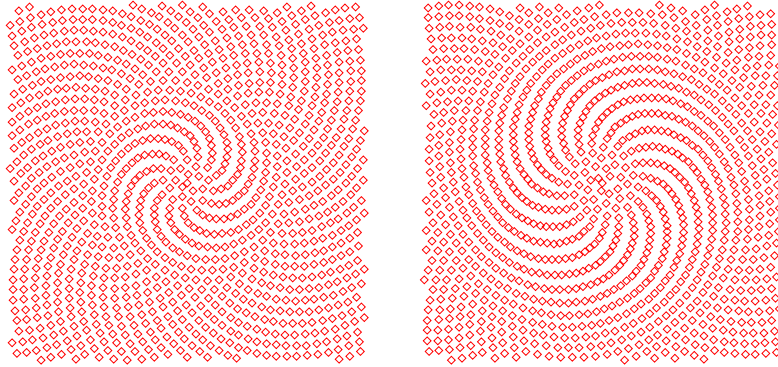


Figure 4: Small points of $\varphi_\theta(\mathbb{N})$ for $\theta = \frac{1765-\sqrt{5}}{2858}$ (left side) and $\theta = e^{-1}$ (right side).

The left half of Figure 4 shows all points of $\varphi_\theta(\mathbb{N})$ with real and imaginary parts smaller than 30 for $\theta = \frac{1765-\sqrt{5}}{2858}$ and $\theta = e^{-1}$. We have $\frac{1765-\sqrt{5}}{2858} = [0; 1, 1, 1, 1, 1, 1, 3, 1, 1, 1, 1, \dots]$ and the first convergents are

$$\frac{0}{1}, \frac{1}{1}, \frac{1}{2}, \frac{2}{3}, \frac{3}{5}, \frac{5}{8}, \frac{8}{13}, \frac{29}{47}, \frac{37}{60}, \dots$$

The 13 parastichy spirals corresponding to the denominator 13 are clearly visible. This is of course due to the “large” coefficient 3 in the continued fraction expansion of θ which leads to three parastichy transitions of type II.

Similarly, we get for the parameter $\theta = e^{-1} = [0; 2, 1, 2, 1, 1, 4, 1, 1, 6, 1, 1, 8]$ corresponding to the right half of Figure 4 the convergents

$$\frac{0}{1}, \frac{1}{2}, \frac{1}{3}, \frac{3}{8}, \frac{4}{11}, \frac{7}{19}, \frac{32}{87}, \frac{39}{106}, \dots$$

with a clearly visible parastichy family corresponding to the denominator 19. This family is due to the large coefficient 4 (the family corresponding to 6 becomes visible at a larger scale) which causes four parastichy transitions of type II.

8.2 Monodromy

One can consider two notions of monodromy for phyllotactic sets:

A first notion consists in moving a chosen basis for the local “lattice” by comparing bases of close points in the obvious way. No monodromy arises in this way: A closed loop gives rise to the identity.

A second, slightly more interesting feature is translational monodromy: going counterclockwise around the origin on a piecewise linear path and stitching the obtained lattice elements (with respect to “bases” which are

“moved” continuously) together, we get at a point $a + ib \in \varphi_\theta(\mathbb{N})$ a vector close to $2\pi(-b + ia)$. More precisely, using a basis V_1, V_2 associated to primary and secondary parastichy spirals, this vector is of the form $(q_{j-1} + kq_j)V_1 \pm q_j V_2$ (with signs depending on the sign conventions for V_1 and V_2) if $\varphi_\theta(\mathbb{N})$ contains q_j primary and $(q_{j-1} + kq_j)$ secondary parastichy families at distance $\sqrt{a^2 + b^2}$ from the origin.

9 Other models

9.1 Cylindric and logarithmic models

In [3] Coxeter, following [2], models the structure of pineapples or pinecones by approximating their shape with a cylinder which he develops on the plane thus getting an infinite strip of a lattice. The visible features (scales) on pineapples are the Voronoi domains of this lattice. The obtained lattice should stay close to the hexagonal lattice which has optimal packing and covering properties. Working with a cylinder of circumference 2π , we have thus to choose the optimal divergence angle $2\pi\theta$ such that the complex lattice $\mathbb{Z} + \mathbb{Z}(\theta + \epsilon i)$ is close to the hexagonal lattice for small ϵ . There is no exact control over the value of ϵ since pineapples or pine cones are not exact cylinders. We should thus choose the value of θ such that the geodesic $t \mapsto \theta + ti$ is overall optimal for small positive ϵ . For a fixed value of θ , the map $\epsilon \mapsto \theta + \epsilon i$ defines again a geodesic of the hyperbolic half-plane.

The best choice is of course again given by $\lambda = \frac{1+\sqrt{5}}{2}2\pi$ (or by its negative) modulo 2π yielding a geodesic which is asymptotically close to the shortest periodic geodesic

$$(0, \infty) \ni t \mapsto \frac{1(1+it) + (-1+it)\sqrt{5}}{2(1+it)}$$

of the modular curve $\mathrm{PSL}_2(\mathbb{Z}) \backslash \mathbb{H}$.

Remark 9.1. *Identifying an infinitely long cylinder of circumference 1 with the quotient space of \mathbb{C} under translations of the form $2i\pi\mathbb{Z}$, the usual exponential function transforms the cylindric model into the logarithmic model with points on a logarithmic ontogenetic spiral defined by $\mathbb{N} \ni n \mapsto \rho^n e^{2i\pi\theta n}$.*

9.2 van Iterson’s disc-packing model

In [5] van Iterson considers periodic packings of equal discs on cylinders such that every disc touches (at least) two pairs of adjacent discs.

Levitov in [8] observes that the associated lattices correspond to elements of norm 1 in the modular domain and that the corresponding Teichmüller space (given by equivalence classes of lattices endowed with a

positively-oriented basis) is a 3-regular tree with mid-edges given by the $\mathrm{PSL}_2(\mathbb{Z})$ -orbit of i (corresponding to the square-lattice) and vertices given by the $\mathrm{PSL}_2(\mathbb{Z})$ -orbit of $\frac{1+i\sqrt{3}}{2}$ (corresponding to the hexagonal lattice). The rooted subtree defined in the quarter-plane of \mathbb{C} defined by all elements of \mathbb{H} with non-negative real parts is then in natural bijection with the so-called Farey-tree. The optimal approximatively straight choice for a path on this rooted tree corresponds of course again to the golden mean and is given by alternating left- and right-turns at every bifurcation, as also observed by Levitov who gives a physical explanation based on energy levels of this fact.

Remark 9.2. *van Iterson's model involves sphere packings which are "locally optimal" in the sense that every disc of the packing (almost) touches four other discs. The associated Voronoi domains have however not asymptotically equal area.*

The model determined by the phyllotactic map φ_θ gives Voronoi domains with asymptotically equal area but leads to discs in the corresponding sphere packing which are almost all isolated. Exceptions are occurring at parastichy transitions of type I (happening asymptotically at the square lattice if θ is the golden ratio).

10 Testing the existence of phyllotactic geodesics in real sunflowers

Phyllotactic geodesics are perhaps a mere mathematical artefact due to the use of the model maps φ_θ . This Section sketches a test probing the reality of the theory.

A first step is of course gathering real data, consisting of a fair number of pictures of large flawless sunflower-capitula. These pictures should be enriched by adding as smoothly as possible (using perhaps splines or trigonometric functions and a least square method) all visible parastichy spirals. Intersections of transversal parastichy spirals should now be taken as the centers of seeds. Points near the center can be neglected.

We can check adequacy of $\varphi_\theta(\mathbb{N})$ for sunflowers as follows: Determine for each picture (endowed with a complex coordinate system) parameters $A \in \mathbb{C}, C \in \mathbb{C}^*, \theta, \gamma \in \mathbb{R}$ giving the best least square approximation of the obtained seed-centers with a suitable set of points of the form

$$\mathbb{N} \ni n \longmapsto A + C\sqrt{n + \gamma} e^{2i\pi\theta n},$$

supposing that the pictures have no distortions (additional parameters are necessary otherwise). If this approximation is nearly perfect, the sunflower map is an accurate description of reality and the existence of phyllotactic geodesics is confirmed. A failure or a bad match does however not contradict the existence of phyllotactic geodesics but forces us to compute points of

“hypothetical” geodesics using the real data-sets instead of the model set $\varphi_\theta(\mathbb{N})$.

This can be achieved as follows: For each point P neither on the boundary nor in the center of the sunflower, we determine pairs of points a, A and b, B adjacent to P with a, A on one parastichy spiral through P and b, B on the other, transversal parastichy spiral through P . The linearized lattice at P is then approximatively given by $\mathbb{Z}\frac{A-a}{2} + \mathbb{Z}\frac{B-b}{2}$. This allows the computation of the corresponding modular invariant by considering the point of the modular curve represented by $\pm\frac{A-a}{B-b}$ (for the unique sign choice leading to a strictly positive imaginary part). Suitable lifts of these points to \mathbb{H} should now lie close to a hyperbolic geodesic which can be guessed by least square approximation.

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