Phyllotaxis on surfaces of constant Gaussian curvature

J F Sadoc¹, J Charvolin¹ and N Rivier²

¹ Laboratoire de Physique des Solides, Université Paris-Sud, CNRS UMR 8502, F-91405 Orsay, cedex, France
² IPCMS, Université de Strasbourg, F-67084 Strasbourg, cedex, France

E-mail: jean-francois.sadoc@u-psud.fr

Received 12 April 2013, in final form 10 June 2013
Published 4 July 2013
Online at stacks.iop.org/JPhysA/46/295202

Abstract
A close-packed organization with circular symmetry of a large number of small discs on a plane is obtained when the centres of the discs are distributed according to the algorithm of phyllotaxis. We study here the distributions obtained on surfaces of constant Gaussian curvatures, positive for the sphere or negative for the hyperbolic plane. We examine how the properties of homogeneity, isotropy and self-similarity, typical of the distribution on the plane and resulting from the presence of circular grain boundaries with quasicrystalline sequences, are affected by the curvature of the bearing surface. The quasicrystalline sequences of the grain boundaries appear indeed to be structural invariants, but the widths of the grains they separate vary differently with the curvature of the surface. The self-similarity of the whole organization observed on the plane is therefore lost on the hyperbolic plane and the sphere. The evolutions of the local order within the grains show no differences except on the equatorial belt of the sphere where the isotropy is decreased owing to the symmetry of this finite surface around its equator.

PACS numbers: 61.30.Cz, 87.15.A, 02.40.k

1. Introduction

The densest organization of small discs on an infinite plane is obtained when their centres are at the nodes of the triangular tiling of the hexagonal lattice. All these discs occupy the same area on the plane and have the same local environment of six equally spaced first neighbours which is reproduced all over the plane according to the laws of classical crystallography. This crystalline solution remains valid for a limited assembly of small discs within a finite compact domain of the plane under the condition that the borders of the domain be aligned along reticular directions of the lattice. If not, as for a circular domain, this solution is no longer valid, the circular symmetry of the domain being not accounted for by the finite number of rotational symmetries of a crystal.
It has been shown that the best packing efficiency found in the case of circular symmetry is obtained when the centres of the discs are regularly placed on the spiral drawn by the algorithm of phyllotaxis [1–3]. This solution approaches circular symmetry, but the area per disc, the number of first neighbours and their distances are no longer constant as they are in the case with hexagonal symmetry. Those differences between crystalline and phyllotactic organizations were recently analysed considering not only the positions of the centres of the discs but also the polygonal nature of their Voronoi cells [10]. Such an analysis shows that the phyllotactic best packing efficiency results from an interplay between metric and topological distortions leading to a structure with an inflation–deflation symmetry. We study here the distributions of points with their Voronoi cells drawn by the algorithm of phyllotaxis onto surfaces of constant Gaussian curvatures, positive for the sphere or negative for the hyperbolic plane. We examine how the best packing efficiency typical of the distribution on the plane evolves with the curvature of the underlying surface, considering both short-range (the shape of a cell, its area and the distances from its centre to the first neighbour points) and long-range characteristics (the repetition law governing the organization of the cells).

In this paper, we show that only the radial part of the phyllotactic pattern (equation (1)) depends on the curvature. The concentric rings of defects have the same structure and the same length, independent of the curvature. Thus, the structural stability of phyllotaxis, based on minimizing strain energy through a succession of structural transitions (through the divergence angle $\lambda$) between successive florets, holds regardless of the curvature [4–9].

The part of this work concerning the plane and spherical phyllotaxis was motivated by our interest in the lateral organizations of long biological molecules in dense fibres with a circular section imposed by their surface tension [11]. These organizations can indeed be represented by distributions of points on planar or spherical bases according to the fact that the molecules can be parallel or twisted within the fibres. Spherical phyllotaxis was also used earlier as a simple ideal approached by vegetal forms [12], in order to obtain the most homogeneous sampling of points on a sphere in the numerical integration [13], to develop climate models of the earth [14] or to estimate the Earth coverage of satellite constellations [15]. We do not know of any application concerning phyllotaxis on surfaces with a negative Gaussian curvature up to now.

Since the distributions on the sphere and the hyperbolic plane will be compared to that observed on the plane, we recall first the main features of the latter, limiting ourselves to what is needed for this comparison, with demonstrations and more details given in [10].

2. Phyllotaxis on the Euclidean plane

The Voronoi cells, used in [10] to describe the phyllotaxis on the plane, are an efficient tool to analyse the geometry and the topology of the structure.

2.1. Pattern

A phyllotactic distribution of points indexed by $s$ is described by an algorithm such that the position of point $s$ is given by its polar coordinates:

$$\rho(s) = a\sqrt{s} \quad \text{and} \quad \theta(s) = 2\pi \lambda s$$

(1)
Figure 1. A set of $n = 3000$ points organized on the plane according to the algorithm of phyllotaxis with the golden ratio. Each point is surrounded by its polygonal Voronoi cell whose number of sides corresponds to the number of first neighbours around the point. Dark, medium and light grey cells are respectively pentagons, hexagons and heptagons. The three spirals joining the first neighbours of the points are called parastichies. The white dot marks the origin point $s = 0$.

which is the equation of a Fermat spiral called the generative spiral hereafter. The parameter $a$ defines the metric scale. Sites, indexed by positive integers $s$, are placed on this spiral$^3$, so that the azimuth between two successive points varies by $2\pi \lambda$. The best packing efficiency is obtained for $\lambda = 1/\tau$, where $\tau$ is the golden ratio $(1 + \sqrt{5})/2$. The Voronoi cell of point $s$ is defined as the region of space nearer to it than to any other point of the pattern. The phyllotactic pattern of a set of 3000 points with their Voronoi cells is shown in figure 1.

In such a pattern, pentagons and heptagons are topological defects distributed among hexagons. These defects appear concentrated in narrow circular rings with constant width, separating large annuli of hexagons whose width increases from the core towards the periphery. In the narrow rings, pentagons and heptagons are paired as dipoles separated by hexagons whose shape is that of a square with two adjacent corners cut off. The defect rings are indeed grain boundaries separating grains of hexagonal cells, each dipole acting as a dislocation that introduces a new parastichy (the lines joining first neighbours) to maintain the density as constant as possible. The underlying arithmetic of this organization is that of the Fibonacci


3 In this paper, the first point corresponds to $s = 0$ and the next to successive integers. Taking $s \in \mathbb{Z} + 1/2$ leads to a more regular structure in the core of the phyllotaxis and it appears as a $\pi/\tau$ rotation for large $s$. 
sequence, $f_u = f_{u-1} + f_{u-2}$ from $f_0 = 0$ and $f_1 = 1$, as summarized in table 1. So cells are organized in concentric blocks, grains separated by grain boundaries, surrounding a central core containing about ten points and showing an apparent disorder recalling the structure of confined two-dimensional foams. In this paper, we are interested in large structures, so that we shall consider what happens outside the core: a succession of large grains of hexagonal cells that are concentric circular annuli, bounded and separated by circular grain boundaries ($f_{u-1}, f_{u-2}, f_{u-1}$) made of $f_{u-1}$ heptagonal cells, $f_{u-2}$ hexagonal cells and $f_{u-1}$ pentagonal cells.

These grain boundaries serve as natural boundaries for our optimal packing problem. Outwards packing begins with the first complete grain boundary (13, 8, 13) with 13 heptagons, 8 hexagons and 13 pentagons. The core is bounded by the eight pentagons of the (first) incomplete grain boundary (3, 5, 8). It has three heptagons instead of the full eight. The additional pentagons (nearly) fulfil the topological requirement that a tiled circular domain should have a topological charge of 6 (i.e. six additional pentagons, a sphere having a

### Table 1.

| $u$  | Cell type | Number of cells | From | To      | Neighbour separations $\delta$s |
|------|-----------|----------------|------|---------|-------------------------------|
| (a)  | Pentagon  | 2              | 0    | 1       | 1, 2, 3, 4, 5 or $-1, 2, 3, 5, 8$ |
|      | Hexagon   | 1              | 2    | 2       | $-2, 2, 3, 5, 8, 13$           |
|      | Heptagon  | 3              | 3    | 5       | $(-3, -2, 2)$ or $(-4, -3, -2)$ or $(-5, -3, -2), 3, 5, 8, 13$ |
|      | Hexagon   | 1              | 6    | 6       | $-5, -3, 3, 5, 8, 13$          |
|      | Pentagon  | 2              | 7    | 8       | $-5, -3, 5, 8, 13$             |
|      | Hexagon   | 1              | 9    | 9       | $-8, -5, -3, 5, 8, 13$         |
|      | Hexagon   | 5              | 10   | 14      | $-8, -5, 5, 8, 13, 21$         |
|      | Heptagon  | 3              | 15   | 17      | $-13, -8, 5, 8, 13, 21$        |
|      | Hexagon   | 5              | 18   | 22      | $-13, -8, -5, 8, 13, 21$       |
|      | Pentagon  | 8              | 23   | 30      | $-13, -8, 8, 13, 21$           |
| (b)  | Pentagon  | 1              | 1    | 1       | 1, 2, 3, 5, 8                  |
|      | Hexagon   | 2              | 2    | 3       | $-1, 1, 2, 3, 5, 8$ or $-2, -1, 2, 3, 5, 8$ |
|      | Hexagon   | 2              | 4    | 5       | $-3, -2, 3, 5, 8, 13$          |
|      | Hexagon   | 3              | 6    | 7       | $-5, -3, 5, 8, 13$             |
|      | Pentagon  | 1              | 8    | 8       | $-5, -3, 5, 8, 13$             |
|      | Hexagon   | 1              | 9    | 9       | $-8, -5, -3, 5, 8, 13$         |
|      | Heptagon  | 1              | 10   | 10      | $-8, -5, -3, 5, 8, 13, 21$     |
|      | Hexagon   | 5              | 11   | 15      | $-8, -5, 5, 8, 13, 21$         |
|      | Heptagon  | 2              | 16   | 17      | $-13, -8, -5, 5, 8, 13, 21$    |
topological charge 12) [8, 17]. This solves the packing efficiency problem: one grain boundary constitutes a perfect circular boundary for the domain into which objects are to be packed.

2.2. Defect rings

In the middle of hexagonal grains it is easy to identify three parastichies which are spirals running through neighbouring points. The three curves intersect with an angle close to $2\pi/3$, but when the spirals approach the grain boundary domain, only two remain apparent. The third disappears to restart in an orthogonal direction through the truncated square hexagons of the grain boundary. The two apparent parastichies are orthogonal and give the directions of the dipoles. The Voronoi cells on the grain boundaries are nearly squares. The two apparent parastichies are orthogonal to the square edges, the third runs along one diagonal only and there is a flip of the diagonal across the hexagons of the grain boundary.

The elementary dipoles (in which heptagons and pentagons are nearest neighbours) are oriented along parastichies $f_u$, denoted by $u$ in table 1, but there is a flip of orientation from one grain boundary to the next. Nevertheless, all dipoles make the same angle $\arccot\left(\frac{fu}{f_{u-1}}\right) \approx \arccot(\tau)$ in an absolute value with the radial direction. This results simply from the description of grain boundaries given in appendix A as a strip in a square lattice.

The perimeter of a ring of dipoles is determined by its number of dipoles and hexagonal cells constituting it. Table 1 shows that this number belongs to the Fibonacci sequence so that the ratio of the radii of two successive rings of dipoles is approximated by the golden ratio $\tau$. Strictly, as shown in appendix A, this ratio is $\sqrt{f_{2u+3}/f_{2u+1}}$ converging to $\tau$ for large Fibonacci numbers. It can be seen in figure 1 that the dipoles occur as singletons, or in pairs, distributed on the ring according to an approximant of a quasicrystalline sequence [23], as explained in appendix A. When moving from one ring to the next, away from the core, the evolution of the sequence is determined by the Fibonacci inflation/deflation rule where a singleton becomes a pair and a pair becomes a pair plus a singleton.

2.3. Metric properties

The area of a disc of radius $\rho$ which contains $s$ points is $\pi \rho^2 = \pi a^2 s$ so that the average area per point has the value $\pi a^2$. The Voronoi decomposition is a tessellation which attributes a specific area to each point. But the areas of Voronoi cells are not all identical as shown in figure 2(a) even if fluctuations are small. The area of a Voronoi cell falls rapidly each time a ring of dipoles is crossed as $s$ increases and it tends towards $\pi a^2$ for large $s$. The fluctuations are small immediately outside the core of the pattern. The histogram describes the level of homogeneity attained with the phyllotaxis. The standard deviations of similar histograms are $\delta = 0.01589$ for $n = 6000$, $\delta = 0.02246$ for $n = 3000$ and $\delta = 0.03171$ for $n = 1500$ (assuming $a = 1$), rapidly decreasing with size $n$.

The behaviour of the distances between first neighbour points is shown in figure 2(b). On grain boundaries where the Voronoi cells are slightly deformed squares, the cell area is approximatively $\pi a^2$ so that the distance between points, along a square edge, is $\sqrt{2} \simeq 1.772$ (with $a = 1$). Whereas along a diagonal, it is $\sqrt{2}\pi \simeq 2.506$. Within the grains, where Voronoi cells are more regular hexagons, the two distances are close to $\sqrt{\frac{\pi}{3}} \simeq 2.053$. The distance between the two points defined by $s$ and $s + f_u$ as a function of $s$ is obtained using the relation (see [10, 19]):

$$d_u(s) = f_u \left( \frac{1}{4s} + \frac{s(-2\pi f_{u-1} + 2\pi \tau^{-1} f_u)^2}{f_u^2} \right)^{1/2},$$

(2)
Figure 2. (a) Variation of the area of Voronoi cells for a pattern of \( n = 3000 \) cells. This is obtained with the scaling parameter \( a = 1 \) in equation (1) leading to an area close to \( \pi \). This area tends towards \( \pi \), but with rapid variations at grain boundaries. Inserted is a histogram of the area of cells. The scale is very inflated. (b) First neighbour distances between points \( s \) and \( s + \delta s \) along parastichies. Black, for the interval \( \delta s \) equal to the smallest positive Fibonacci number in the list of table 1. Dotted, for the next interval, grey for the third positive interval and dark for the last one (occurring only if the Voronoi cell is a heptagon). So black, dotted and grey correspond to the distance along the three visible parastichies. Each continuous curve corresponds to a given Fibonacci number that appears in different rings. For instance, \( f_{11} = 55 \) appearing between \( s = 101 \) and 2254 yields a continuous curve which is successively dark grey, grey, dotted and black. Lower and upper crossings of two curves correspond to a grain boundary, other crossings are in the middle of a hexagonal grain. A histogram of all distances is inserted. The hook for distances close to \( 1.9 \) and 2.3 is an artefact due to the finite number of points. The distances lie in the range \( [(2\pi/\sqrt{5})^{1/2}, (2\pi)^{1/2}] \).

this relation\(^4\) fits the numerical values given in figure 2(b). It can be verified that minimal values are

\[
\sqrt{2\pi} f_u \sqrt{\frac{1}{\tau} - \frac{f_{u-1}}{f_u}}
\]

(3)

all close to and converging towards \( \sqrt{\frac{2\pi}{\sqrt{5}}} \simeq 1.67 \). The first neighbours distances are in the range \( \left[ \sqrt{\frac{2\pi}{\sqrt{5}}}, \sqrt{2\pi} \right] \), for all \( s \) and \( u \). This property, generic to the choice of \( \lambda = 1/\tau \) (or any noble number) is crucial to ensure the best isotropy. The reason is that \( \tau \) is gently approximated by successive truncations of its continued fraction (containing only 1), which are the ratios of two successive Fibonacci numbers and so converging smoothly [21, 22]. It is this property which leads to minimal values for distances given by equation (3) converging towards a finite value. Other irrationals (with a continued fraction expansion containing other integers) introduce distances between neighbours decreasing more rapidly with \( \delta s \).

\(^4\) This relation assumes that \( \delta s \) is infinitesimal compared to \( s \). An estimation of the accuracy can be obtained by comparing the distance computed between points \( s \) and \( s + \delta s \) with that between \( s - \delta s \) and \( s \). They should be equal but computed values differ very slightly. The mean is very accurate.
Figure 3. Hyperbolic phyllotaxis represented inside the Poincaré disc. The pattern is obtained using equation (4) with 3000 points and $a = 1/20$. Dark, medium and light grey cells are respectively pentagons, hexagons and heptagons. All areas and distances are scaled so that the mean area per points is $\pi$. With this choice, the curvature $\kappa = -1/R^2$ is given by $R = 1/a$, with the parameter $a = 1/20$. In the Poincaré disc representation, the cell size seems to decrease in approaching the limit circle.

3. Phyllotaxis on the hyperbolic plane

3.1. The Poincaré disc

The Poincaré disc model is a simple way to represent the hyperbolic plane as presented in appendix B. A point in the hyperbolic plane is defined by polar coordinate $(\rho, \vartheta)$ and is represented on the Poincaré disc by $(r, \vartheta)$, where distances are obtained with a specific metric $d\sigma^2 = 4(dr^2 + r^2d\vartheta^2)/(1-r^2)^2$. So $r = 1$ represents points at infinity. This metric has the form of a Euclidean metric in polar coordinates divided by a function of $r$ only: it is locally a Euclidean metric.

3.2. Pattern

As for the phyllotaxis in the Euclidean plane, a point is defined by an integer $s$ on a spiral and the pattern obtained is shown in figure 3. The number of points in a hyperbolic cap of radius $\rho(s)$ is proportional to $s$. We choose the function $\rho(s)$ so that the number of points contained
in the domain is $\pi a^2 s$, as it is for the Euclidean plane phyllotaxis. Using equation (B.1) given for the area enclosed by a circle in appendix B, we write $2\pi a^2 s/2 = 2\pi (\cosh \varphi - 1)$, with $R = 1$ to have Gaussian curvature $\kappa = -1$, then $\varphi = \rho(s)$. The true radius in the hyperbolic plane is $\rho(s) = \cosh^{-1} \left( \frac{e^\varphi}{2} + 1 \right)$. This radius is a length measured on the hyperbolic plane, but on the Poincaré disc, the Euclidean distance from the origin to the representation of a point $r = \tanh(\varphi/2)$ is given by

$$r(s) = \tanh \left( \frac{1}{2} \cosh^{-1} \left( \frac{a^2 s}{2} + 1 \right) \right).$$

The factor $a^2/2$ relating $s$ and $\rho(s)$ yields the radius in the hyperbolic plane $\rho(s) \approx a\sqrt{s}$ for small $s$ as in the flat phyllotaxis. The spiral equation in the hyperbolic plane is

$$(\rho(s) \cos(2\pi \lambda s), \rho(s) \sin(2\pi \lambda s)),$$

where $\lambda$ is a similar parameter as in the plane phyllotaxis. Accordingly, the true hyperbolic phyllotaxis corresponds to the choice $\lambda = 1/\tau$. As shown in section 3.4, the $\rho(s)$ behaviour and the choice of $\lambda = 1/\tau$ ensure the best homogeneity and isotropy for the distribution of points.

### 3.3. Rings of dipoles

A Voronoi decomposition of the phyllotaxis mapped on the Poincaré disc can be obtained as if the structure in this disc was Euclidean. This is justified by the fact that the metric is locally Euclidean. If two points are hyperbolic neighbours, they are also neighbours using the local Euclidean metric on the Poincaré map. In figure 3, Voronoi cell edges are straight segments; on an exact Voronoi decomposition they should be arcs of circles representing geodesic lines of the Poincaré disc but as these segments are very short, the approximation is clearly good.

As in the plane phyllotaxis, it is possible to define hexagonal grains separated by grain boundaries consisting of pentagon–heptagon dipoles and isolated hexagons. It is the change in the separations $\delta s = f_{u-1} - f_u, f_{u+1}$ between neighbours in one grain and the next which governs a grain boundary. So the description given in appendix A is unchanged, still related to Fibonacci numbers. Grain boundaries have indeed the same structure in the three examples of phyllotaxis.

### 3.4. Metric properties in hyperbolic phyllotaxis

The function $\rho(s)$ has been chosen so that $\pi a^2 s$ is the area enclosed by a circle of radius $\rho$ on a hyperbolic plane of Gaussian curvature $\kappa = -1$. In figure 4(a), the evolution of the area per cell is shown scaled to have mean area equal to $\pi$ as in the Euclidean case; so the curvature is $\kappa = -1/R^2$ with $R = 1/a$. Area fluctuations are stronger, with smaller damping than in the plane case.

The distances between first neighbour points can be obtained directly from the coordinates, as shown in figure 4(b), but one can have an analytic relation between the distances and $s$. On a plane representation, the distance, measured on the plane, separating two neighbour points whose indices are $s$ and $s + \delta s$ with $\delta s = f_u$ is given with good accuracy by:

$$d_u(s)^2 = f_u^2 \left[ r(s) + \left( \frac{\gamma u}{f_u} \right)^2 r(s)^2 \right],$$

where $r(s)$ is the true radius in the hyperbolic plane.

---

5 More precisely, this is also related to the fact that two triangular Delaunay decompositions obtained using the Euclidean metric of the plane representation or the hyperbolic metric are formed with the same set of triangles. These triangles are defined so that their circumcircles do not enclose any other points of the phyllotaxis. Consequently, neighbourhood relations are the same in the two metrics.
Figure 4. Area and distances on the hyperbolic plane. All areas and distances are scaled so that the mean area per point is $\pi$. With this choice the curvature $\kappa = -1/R^2$ is given by $R = 1/a$, with the parameter $a = 1/40$. (a) Areas of Voronoi cells for the hyperbolic phyllotaxis. The area is close to the mean value $\pi$, with strong fluctuations within defect rings. Nevertheless, these fluctuations decrease as the area tends towards $\pi$ for large $s$.

(b) Distance between point $s$ and its first neighbours $s + \delta s$ with positive $\delta s$. Grey, dotted and black correspond to the distance along the three visible parastichies. Distances are confined between the limits $\sqrt{2}\pi$ and $\sqrt{2}\pi/\sqrt{5}$.

with $\gamma_u = (-2\pi f_{u-1} + 2\pi \tau^{-1} f_u)$ and $r(s)$ given by equation (4). Equation (2) given for a plane phyllotaxis is derived from this equation (see the footnote in 2.3 on the accuracy of this relation), but to have the true hyperbolic distances requires taking account of a correction factor to the metric. This factor is $1/(1 - r(s)^2)$. Then the distances are given by:

$$d_u(s) = f_u \frac{1}{1 - r(s)^2} \left( \frac{-a^2}{4s(1 + sa)^2} + \frac{r(s)^2(-2\pi f_{u-1} + 2\pi \tau^{-1} f_u)^2}{f_u^2} \right)^{1/2}.$$  

This relation fits the curves given in figure 4(b) after normalization by a scaling factor $1/a$ in order to have mean area of cells equal $\pi$.

Since the sequence of rings of dipoles is independent of the curvature, as developed in appendix A, the sole effect of the negative curvature is to decrease the width of the hexagonal grains that tends to a constant for large $s$. Indeed, the radius of a grain boundary is $\sinh \varphi_u = \sqrt{f_{2u+1}/\pi}/2$, which behaves for large $u$ as $\varphi_u \simeq \ln(\sqrt{f_{2u+1}/\pi})$. The annular grain bounded by the grain boundaries $(u - 1)$ and $(u)$ has width $\varphi_u - \varphi_{u-1} \simeq \ln(\sqrt{f_{2u+1}/f_{2u-1}}) \simeq \ln \tau$.

As on the plane, the maximum for first neighbour distances is still $\sqrt{2\pi} \simeq 2.506$, corresponding to square-like cells with a distance related to the diagonal. The minimal values of $d_u(s)$ (equation (6)) are $\sqrt{2\pi} f_u \left[ \frac{1}{\varphi_u} - \frac{1}{\varphi_{u+1}} \right]$ very close to and converging towards $\sqrt{\frac{2\pi}{\sqrt{3}}} \simeq 1.67$. Distances are confined in the same domain as for the plane phyllotaxis, a consequence of the choice of the parameter $\lambda = 1/\tau$.

4. Phyllotaxis on the sphere

4.1. Pattern

The algorithm used to build the phyllotactic configurations shown in figure 5 is such that the position of point $s$ is given by the spherical coordinates $(\rho, \phi, \theta)$. These coordinates are $\rho = R$, the sphere radius, $\theta = 2\pi \lambda \nu$, the azimuthal angle, and $\phi = \arcsin(s'/\nu) + \pi/2$, the polar angle. The total number of points on the sphere is $n = 2\nu + 1$. With this choice, the integer $s'$ goes from $-\nu$ to $\nu$ with $s' = -\nu$ or $s' = \nu$ for points on poles, and $s' = 0$ for a point
Figure 5. Phyllotaxis on a sphere with 4001 points. Dark, medium and light grey cells are pentagons, hexagons and heptagons; the white dot marks a pole. The rings of dipoles appear clearly. Around the equator, there is a large hexagonal domain even though the cells look like squares; in fact they have six edges, two of which being very small. The structure has chiral symmetry around the axis joining the two poles. The equator mid-point $s = 2000$ is a point of symmetry of order 2.

on the equator. For comparison with the plane phyllotaxis, it could be helpful to have $s = 0$ on the north pole using $s = s' + \nu$.

The spherical phyllotaxis is obtained by mapping of points on a finite cylinder which is tangent to the sphere along the equator, so which has the same radius $R$ and whose finite height is $2R$. The area of this finite cylinder is the same as that of the sphere, namely $4\pi R^2$. The points on the cylinder are located on a perfect helix defined by $\theta = 2\pi \lambda s$ and a pitch related to the number of points on the sphere. They can be considered as a perfect crystal without a defect wrapped on the cylinder, so with a constant density of points. This is an example of phyllotaxis on a cylinder as described in [20, 5]. With $\lambda = 1/\tau$, a point $s$ has six neighbours at position $s \pm \delta s$ with $\delta s$ equal to three successive Fibonacci numbers, depending on the pitch of the helix drawn on the cylinder. These points are mapped on the sphere orthogonally to the polar axis and so the area per points on the sphere is the same as on the cylinder. This results from the property of the area of a spherical zone enclosed on a sphere of radius $R$, between two parallel planes at distance $h$ to be the same as the area of a finite part of a cylinder of radius $R$ enclosed between the two same parallel planes orthogonal to the cylinder axis. This justifies the choice of the polar angle on the sphere $\phi = \arcsin(s'/\nu) - \pi/2$ deduced from the cylindrical coordinate $(R, \theta, R \sin(\phi + \pi/2))$. But the projection on the sphere, even if it conserves area, introduces inhomogeneous shearing in the structure. This shearing, at constant area, is given by a compression factor $\cos(\phi)$ changing the equator length into a parallel length.
(at \(\phi\)), and an expansion factor \(1/\cos(\phi)\) along meridians. This shearing could change the incidence relations between neighbours so first neighbours are not necessarily the same as on the ‘crystalline’ cylinder and defects appear. The area associated with cells is close to constant as in the plane phyllotaxis. The choice of \(R\) is arbitrary but in order to have cell area close to \(\pi\) as in the plane phyllotaxis \(R = \sqrt{2v + 1}/2\).

A Voronoi decomposition of the set of points on the sphere reveals the phyllotaxis and how defects appear\(^6\). As in plane phyllotaxis, the Voronoi cells are hexagons, pentagons or heptagons, with most of the Voronoi cells being hexagons. We call the large domains with only hexagonal Voronoi cells hexagonal grains, even if they are not regular, and the circular distribution of heptagonal, hexagonal and pentagonal cells are grain boundaries.

### 4.2. Rings of dipoles

The number of rings of dipoles depends on the number \(n\) of points on the sphere, related to its radius \(R = \sqrt{n}/2\). Figure 6 shows how new dipoles appear when \(n\) is increased. The evolution of rings of dipoles is related to the most important fact that the distributions of dipoles and hexagonal cells along these rings follow the one-dimensional sequences approximant of quasicrystals as developed in appendix A. The number of cells in these rings is \(2fu + fu−1 = fu+2\), where \(fu\) is the number of dipoles and \(fu−1\) the number of hexagons. The length of the circle defining a ring of defects is the length of the strip in a square lattice, so that this length is the same in the plane and spherical phyllotaxis. It is \(\sqrt{(fu^2 + fu^2)\pi} \approx \sqrt{2fu+1}\pi\) if we suppose an area per cells given by \(\pi\) and then a cell edge length of \(\sqrt{\pi}\) when cells are squares. Here and in the following, we set the sphere radius \(R = \sqrt{2v + 1}/2\) in order to have an average cell area equal to \(\pi\) as in the plane phyllotaxis. This is then used to estimate the number of cells in hexagonal grains.

On a sphere of radius \(R = \sqrt{2v + 1}/2\) containing \(n = 2v + 1\) sites, a circle defined by the polar angle \(\phi\) borders a spherical cap containing \(v(1 - \cos(\phi))\) sites. If the circle corresponds to a grain boundary of length \(\sqrt{2fu+1}\pi\), this leads to a polar angle \(\phi\) given by \(\sin(\phi) = \sqrt{fu+1}/(2v + 1)\pi\). Thus, the number of points enclosed inside the spherical cap bordered by the grain boundary is \(v(1 - \sqrt{1 - fu+1/(2v + 1)\pi})\).

This is an estimate. In order to obtain the size of the hexagonal grains, we must estimate the width of the grain boundary and equate it to the mean of the \(fu−1\) hexagonal cells in the grain boundary. An estimate for the Voronoi cell numbers \(s\) at the beginning and at the end of a grain boundary is:

\[
\left(5 - fu-1 \right)/2 + v \left(1 - \sqrt{1 - fu+1/(2v + 1)\pi} \right) \cdot \left( fu-1 + 3 \right)/2 + v \left(1 - \sqrt{1 - fu+1/(2v + 1)\pi} \right).
\]  
(7)

This estimate is sometimes off by 1.

By increasing the number \(n\) of points on the sphere, and so decreasing the curvature, new rings of dipoles (grain boundaries) appear on the equator \(\phi = \pi/2\). These are shown in figure 6 in the range \(n \in [1331, 1351]\). New grain boundaries appear as a pair: one in each hemisphere. Just after their appearance, the two grain boundaries are interpenetrating; this introduces some cells with four edges. Setting \(\sin(\phi) = 1\) gives the critical number \(n_{\text{crit}} = \lceil fu+1/\pi \rceil\)

---

\(^6\) The Voronoi decomposition of a set of points on a sphere has been done using a 3D Voronoi analysis considering the set of points on the sphere to which is added the centre of the sphere. Then Delaunay tetrahedra are obtained. They are formed with Delaunay triangles on the sphere surface completed by the centre of the sphere. The Voronoi decomposition on the surface is deduced from this Delaunay triangulation of the surface.
Figure 6. Evolution of rings of defects near the equator with increasing number $n = 2\nu + 1$ of points on the sphere. Voronoi cells are medium grey for hexagons, light grey for heptagons and dark grey for pentagons. Appearing on the equator, they are two interpenetrating rings. Then some cells having only four sides appear in white. A grain boundary on the equator not seen for $n = 1331$ appears with $n = 1333$, so the threshold is just over $n = 1331$.

of points on the sphere for a new grain boundary to appear on the equator. Typically, $n_{\text{crit}} = (\ldots, 74, 194, 508, 1331, 3484, 9122, 23881, \ldots)$. When a new grain boundary $(f_{2\nu+1})$ appears on the equator (for $n_{\text{crit}}$), the previous one $(f_{2\nu-1})$ enters a polar cap at an angle $\phi$ given by $\sin \phi = \sqrt{\frac{f_{2\nu-1}}{n_{\text{crit}}}}$, thus $\sin \phi = \sqrt{\frac{f_{2\nu-1}}{f_{2\nu+1}}}$. It results that $\phi \simeq \arcsin \tau^{-1}$, about 0.666 rad.

This value of $\phi$ does not depend on $n$ as soon as $\sqrt{\frac{f_{2\nu-1}}{f_{2\nu+1}}} \simeq \tau^{-1}$ is a good approximation.

The same evolution repeats itself quite regularly at each appearance of a new grain boundary as shown in figure 7. Using a semi-logarithmic horizontal scale, the curves can be translated from one to the next.

4.3. Metric properties on the sphere

Figure 8 shows that, each time the number $n$ of points on the sphere is translated from one value to the next along the logarithmic scale of figure 7, the distances between first neighbour points are reproduced while a new grain boundary is introduced. Local distances and areas vary within the same limits whatever the number of points. Far away from grain boundaries, the areas are close to the mean value $\pi$ corresponding to the choice $R = \sqrt{n}/2$. There are strong variations crossing grain boundaries near the poles which decrease rapidly.
Figure 7. (a) Evolution of the polar angle $\phi$ of grain boundaries with the number $n$ of points on spheres (logarithmic horizontal scale). Each curve corresponds to grain boundaries defined by $u = 6, 7, 8, 9, 10, 11, 12, 13$. For a given number $n$ (or a given radius $R = \sqrt{n}/2$), there is a grain boundary near the equator if there is a curve such that $\phi \simeq \pi/2$. The two black points (on the curve $\phi$ corresponding to $u = 9$ and $u = 11$) refer to the two examples of spheres whose cell area and distances are given in figure 8. (b) Evolution, with the Gaussian curvature, of the arc length which is the radius of grain boundaries (for instance $R\phi$ in the spherical case). There is a limit to these curves in the spherical case corresponding to the appearance of grain boundaries at the equator.

Figure 8. (Left) Area of Voronoi cells for the spherical phyllotaxis. All areas and distances are scaled so that the mean area per points is $\pi$. Two examples are given with $n = 9301$ and $n = 1351$ points on the sphere. (Right) For the same spheres, distance between point $s$ and its first neighbours $s + \delta s$ with positive $\delta s$ in the northern hemisphere and negative $\delta s$ in the southern. Light, dark and medium grey correspond to the distance along these three visible parastichies. Distances are in the limits $\sqrt{2\pi}$ and $\sqrt{2\pi}/\sqrt{5}$. Curves for the two examples $n = 9301$ and 1351 look very similar, mainly for distances: this is because the $n$ values are chosen to have grain boundaries at the same angular positions as given in figure 7.
In the hyperbolic case, we evaluated distances in the Poincaré representation using a given metric. It is convenient to use a similar method for the spherical space using a representation of the sphere as described in appendix C, which is simply a stereographic projection of the sphere on a tangent plane. On this plane representation of spherical phyllotaxis, the distance separating two neighbour points labelled by \( s \) and \( s + \delta s \) with \( \delta s = f_u \) is always given by equation (5), but where \( r(s) \) is given by equation (C.1). With equation (5) this distance is evaluated with the plane metric, so to have the true distances on the sphere needs to take account of a correcting factor to the metric which is \( 1/(1 + r(s)^2) \) as given in appendix C by equation (C.2). Then the distances are given by:

\[
d_u(s) = f_u \frac{1}{1 + r(s)^2} \left( \frac{-a^2}{4\pi(-1 + sa^2)} + \frac{r(s)^2(-2\pi f_{u-1} + 2\pi \tau^{-1} f_0)^2}{f_u^2} \right)^{1/2}.
\] (8)

This analytical expression fits the distances presented in figure 8 obtained from coordinates of the spherical phyllotaxis taking account of a scaling factor \( 1/\alpha \) in order to have mean area of cells equal \( \pi \). The important conclusion is that these distances are again confined within the same domain as for the plane phyllotaxis. Like in the case of the plane, the maximum for the distance is still \( \sqrt{2\pi} \approx 2.506 \) corresponding to nearly square cells with a distance corresponding to the diagonal. It can be checked that minimal values of \( d_u(s) \) (equation (8)) are \( \sqrt{2\pi} f_u \left| \frac{1}{\tau} - \frac{2\omega}{f_u} \right| \) very close to and converging towards \( \sqrt{\frac{2\pi}{\tau^2}} \approx 1.67 \) as for the plane phyllotaxis. As in the plane and hyperbolic cases, it is this confinement of distances which is the signature of the best uniformity in all orientations.

5. Conclusion

The spiral organization generated by the algorithm of phyllotaxis with the golden ratio ensures the best packing efficiency of points on a plane in a situation of circular symmetry [3]. We examined here whether this simple scheme is affected if the substrate has a positive or negative Gaussian curvature, limiting ourselves to curvature radii much larger than the mean distance between points.

Figures 1, 3 and 5 show that the phyllotactic patterns always present the same appearance. They are all made of a core, without any obvious discernable order [18], surrounded by an ordered series of alternate concentric rings. The cores are the same, they occupy a limited region around the centres of the patterns where the curved surfaces can be assimilated to their tangent plane. The alternate concentric rings are respectively large rings, or grains, made of points with six first neighbours and narrow rings, or grain boundaries, containing also points with five and seven first neighbours associated in dipoles, or dislocations. These topological defects are needed to keep the density as constant as possible in this situation of circular symmetry.

A direct inspection of the grain boundaries makes apparent the fact that they are independent of the curvature. Indeed, only the radial part of the phyllotactic pattern depends on the curvature. The azimuthal part only depends on the parameter \( \lambda = 1/\tau \). The number, distribution and orientation of dipoles on each grain boundary, as well as their evolution from one to the next, do not depend on the curvature of the surface, their perimeters just follow the Fibonacci series as shown in table 1. This directly proceeds from the mathematical structure of the algorithm of phyllotaxis with the golden ratio as developed in appendix A. Figure A1 shows indeed that the dipoles are organized along a grain boundary according to a quasicrystalline sequence whose evolution from one grain boundary to the next is driven by
a well-defined inflation/deflation rule [16, 23]. The distributions of the whole set of points on surfaces of different curvatures must respect this most remarkable structural invariance of the grain boundaries as developed in the following paragraphs.

As the perimeter of successive grain boundaries is constrained to follow the Fibonacci series, the distance between them on the surfaces, or the widths of the grains they enclose, vary differently according to the sign of the curvature. If we call \( P \) the perimeter and \( R \) the radius of curvature, the radii of the grain boundaries indeed varies as \( P/2\pi \) on the plane, \( R \sin^{-1}(P/2\pi R) \) on the sphere and \( R \sinh^{-1}(P/2\pi R) \) on the hyperbolic plane and the width of a given grain decreases as the curvature goes from a positive to a negative value. This results in the more or less rapid dampening of the area per cell around \( \pi \) visible in figures 8, 2 and 4.

Because the dipoles on the grain boundaries have well-defined alternate orientations relative to the radius vector with an angle close to \( \pi/2 - \tan^{-1}(\tau) \), the anchoring conditions of the parastichies at the two limits of any grain are the same whatever the curvature of the surface and the width of the grain. This constraint manifests itself by the fact that the distances between first neighbours oscillate, along more or less extended horizontal scales, between the same limits and cross each other at the same level on the whole plane and hyperbolic plane as shown in figures 2 and 4. However, on the sphere, such oscillating behaviour is observed on a limited polar cap only and not around the equator, as shown in figure 8. This holds to the fact that, when two new grain boundaries merge along the equator, their dipoles are parallel and stay parallel as they move towards their pole as the sphere grows. The anchoring conditions of the parastichies in the grain surrounding the equator do not alternate as they do in other grains and the shape of its Voronoi cells evolves differently than in normal grains. Figures 5 and 6 show that cells in the equatorial belt may keep a shape close to that of a square rather than becoming hexagonal as in normal grains.

Finally, owing to the inflation/deflation rule determining the quasicrystalline sequences of the grain boundaries they form by themselves a self-similar set which is scale invariant as the characteristic distance is changed by a factor which is an approximant of \( \tau^n \). When on the plane, this self-similarity is transferred onto the pattern as, assimilating grain boundaries with ideal circles, their perimeter vary as successive approximants of \( \tau \) and the area of the grains vary as \( \tau^{2n} \). This is however not valid on the sphere or the hyperbolic plane where the area of the grains does not follow a variation in \( \tau^{2n} \).

Appendix A. Grain boundaries and inflation--deflation symmetry

The way dislocation dipoles are organized along circles is strongly related to 1D quasicrystals [23]. A Fibonacci 1D quasicrystal can be obtained using an inflation–deflation rule iteratively applied to a sequence of long and short segments. This inflation–deflation rule is \( L \rightarrow L + S \) and \( S \rightarrow L \). Starting simply from a short segment, this specific rule gives a quasicrystal after an infinite number of iterations, or with a given number of iterations, a finite structure with a number of short and long segments given by two successive Fibonacci numbers. Consider now dipoles formed by a heptagon and a pentagon in contact along grain boundaries. There are isolated dipoles, singletons and pairs of close dipoles. The application of the rule changes a singleton into a pair of dipoles and changes a pair of dipoles into a pair and a singleton, and transforms one ring of dipoles into the next one. So, there is an inflation–deflation symmetry associated with a radial change relating defects in this structure. This can be checked counting the number of pairs of dipoles or of isolated dipoles which are successive Fibonacci numbers, on circles of defects.

In one dimension, quasicrystals can be obtained by the cut and projection method, selecting the points of a square lattice falling inside a strip defined by translation of a cell of the lattice.
Figure A1. Strip cut in a square lattice. This strip is a good approximation of the ring of defects containing 55 points. The aspect of the points corresponds to their type of Voronoi cells: hexagon (open circle), heptagon (light) and pentagon (dark). The first point in light grey is lowest, then points are numbered, increasing by 21 going up or by 34 going left. This strip can be divided into three strips of heptagons, hexagons and pentagons.

along a straight line of slope \( \tau \). Approximants are obtained when the slope is a convergent of \( \tau \) given by the ratio of two successive Fibonacci numbers. Figure A1, which describes how a grain boundary can be derived from a selection of points in a square lattices, is similar to the cut and projection method applied to approximants.

The description of grain boundaries as a strip of squares, allows their lengths to be estimated. Consider, as in the text, an edge length \( d = \sqrt{\pi} \) for a square of area \( \pi \). The length of the grain with \( f_{\mu+1} \) dipoles is the modulus of the vector \((f_\mu, f_{\mu+1})\) which is \( L = \sqrt{\pi(f^2_\mu + f^2_{\mu+1})} \equiv (f_{2\mu+1}\pi)^{1/2} \). Folding the strip into a ring, this length is the
perimeter of a circle, then it is possible to estimate the number of points of the phyllotactic pattern in the domain enclosed by this circle.

Dipoles oriented along parastichies (labelled by \( u \) in table 1) make nearly the same angle with the radial direction (in absolute value as their orientations alternate). Considering the description of grain boundaries by a strip in a square lattice (figure A1), dipoles are represented along square edges and make a constant angle with the large strip side related to the slope of the strip \( f_u/f_{u-1} \). The angle with the normal to the strip is \( \cot^{-1}(f_u/f_{u-1}) \approx \cot^{-1}(\tau) \approx 0.5535 \text{ rad} \). This is also the angle of a dipole with the radial direction for a strip refolded into the ring of a grain boundary if we consider that resulting distortions are small. In fact this is exactly the angle with the radial direction done by the parastichies \( u \) through the medium point of the grain boundary, whatever the curvature.

There are two correlated properties of inflation–deflation symmetry related to grain boundaries. The first one is the organization of dipoles on a grain boundary which is like an approximant. The other aspect, developed in [10], relates one grain boundary to the next. There are a symmetry mixing spiral symmetry and inflation–deflation symmetry associating the two grains. Nevertheless, such a symmetry needs the scale invariance of the plane and cannot be considered in curved geometries. In the plane geometry, the ratio of the radius of two successive grain boundaries is \( \sqrt{f_{2u+1}/f_{2u-1}} \) converging towards \( \tau \) for large Fibonacci numbers. This is a consequence of the inflation–deflation symmetry in the plane geometry. The structure of a grain boundary is only related to its rank \( u \) through Fibonacci number \( f_u \) and does not depend on the space curvature. It is the same for the spherical, plane and hyperbolic phyllotaxis.

Appendix B. The Poincaré disc representation of the hyperbolic plane

The Poincaré disc model, also known as the conformal disc model, is a simple way to represent the hyperbolic plane. It is a mapping of the whole hyperbolic plane on the interior of a disk, so that the limit circle represents infinity. It is a conformal mapping that respects angles between geodesic lines which are represented by arcs of circles that are orthogonal to the limit circle [24, 25].

A method to introduce the hyperbolic plane and its representation is to refer to the spherical geometry and change the Gaussian curvature \( \kappa = 1/R^2 \) into \(-1/R^2\), where \( R \) is the radius of curvature of the surface. By analogy with the equation of a sphere embedded in the Euclidean 3D space, it may be tempting to write \( x^2 + y^2 + z^2 = -R^2 \) with an imaginary radius, but the hyperbolic plane cannot be entirely embedded in \( \mathbb{R}^3 \). So we need a representation of the hyperbolic plane by a surface with a given metric. A good example is given by the Minkowski plane. Consider a 3D vector \( \mathbf{y} = (y_0, y_1, y_2) \) in a 3D space with a metric such that the squared modulus of the vector is \( y^2 = -y_0^2 + y_1^2 + y_2^2 = -R^2 \). The equation \(-y_0^2 + y_1^2 + y_2^2 = -R^2 \) defines a two-sheet hyperboloid. A single sheet, with the appropriate metric, is a model of a surface, with Minkowski metric, whose Gaussian curvature is \(-1/R^2 \). Geodesics on this surface are intersection lines between the hyperboloid and planes through the origin.

Using polar coordinates to describe the \( \mathbf{y} \) vector, we have \( y_0 = R \cosh \varphi, y_1 = R \sinh \varphi \cos \theta, y_2 = R \sinh \varphi \sin \theta \) for points on a sheet. The Minkowski metric \( d\sigma^2 = -dy_0^2 + dy_1^2 + dy_2^2 \) is with polar coordinates \( d\sigma^2 = R^2(d\varphi^2 + \sinh^2 \varphi d\theta^2) \). By comparison with the spherical geometry, it is interesting to note that if we change variables into complex variables \( (y_0 = \eta_0, y_1 = i\eta_1, y_2 = i\eta_2) \) and \( \varphi = i\phi \), the metric looks like the usual metric of a sphere \( d\sigma^2 = R^2(d\phi^2 + \sin^2 \phi d\theta^2) \). In the spherical geometry, the parameter \( R \) is the radius of the sphere. In the hyperbolic geometry, \( R \) cannot be considered as a radius of curvature, it is only the Gaussian curvature \( \kappa = -1/R^2 \), which is an intrinsic property of the surface.
Figure C1. Stereographic projection of a spherical phyllotaxis (part). This is obtained using equation (C1) with 2000 represented points and $a = 1/40$ so the total number of points on the sphere is 6400. By an effect of the projection, the size of the projection of cells seems to increase going outwards, diverging for $n = 6400$.

The Poincaré disc representation is obtained by stereographic projection of one hyperboloid sheet onto the plane $(y_1, y_2)$ with a projection pole $(y_0 = -1, y_1 = 0, y_2 = 0)$. We consider polar coordinates $(r, \vartheta)$ in the plane $(y_1, y_2)$ (that is in the Poincaré disc). The stereographic projection gives $r = R \sinh \varphi/(1 + y_0)$ or $r = R \tanh(\varphi/2)$. Using hyperbolic trigonometric identities, the metric is found to be $\text{d}\sigma^2 = 4R(dr^2 + r^2d\vartheta^2)/(1 - r^2)^2$. This metric has the form of a Euclidean metric in polar coordinates divided by a function of $r$ only: it is locally a Euclidean metric, a confirmation that the representation is conformal.

In order to obtain the equation of the spiral enabling us to build a phyllotaxis on the hyperbolic plane, we need the area enclosed in a circle of given radius $R \varphi_\rho$. This area is obtained using this metric. The perimeter of the circle centred at the origin is $2\pi R \sinh \varphi$ and so the area enclosed by this circle is $\int_0^{\varphi_\rho} 2\pi R^2 \sinh \varphi d\varphi$ which is:

$$2\pi R^2 (\cosh \varphi_\rho - 1). \quad (B.1)$$

Appendix C. A plane representation of the spherical phyllotaxis

There is another way to describe the spherical phyllotaxis by analogy to the hyperbolic one, simply changing the hyperbolic trigonometry into the spherical trigonometry. This gives a representation on the plane of a spherical phyllotaxis, with an adjusted metric as shown in
figure C1. In fact it is a stereographic projection of the tiled sphere onto a tangent plane through the north pole from a projection point on the south pole.

The radial position for a point is given on the plane by

$$r(s) = \tan \left( \frac{1}{2} \cos^{-1} \left( 1 - a^2 s^2 / 2 \right) \right).$$  \hspace{1cm} (C.1)

This radial value is the radial coordinate on the plane and the true spherical distance from the origin to the point depends on the spherical metric:

$$d\sigma^2 = 4 (d\rho^2 + \rho^2 d\theta^2) / (1 + \rho^2)^2.$$ \hspace{1cm} (C.2)

This is a metric which has the form of an Euclidean metric in polar coordinates divided by a function of $r$ only. This is useful to calculate distances: they are calculated as Euclidean distances on the representation, then corrected using the $r$ function. This is a good approximation if distances remain small compared to the radius of curvature. This locally Euclidean metric is related to the fact that the stereographic projection on the plane of the spherical tiling is conformal. The azimuthal position is the same as in the plane case: $2\pi s/\tau$ with $\lambda = 1/\tau$.

Comparing the Euclidean plane case to the plane representations of curved spaces like the Poincaré disc in the hyperbolic case or the stereographic map of the sphere, the main difference is the behaviour of the radial part $r(s)$ of the spiral equation. Evidently, if we consider the usual metric of the plane, and not the given metric of the representations, the size of cells increases in the stereographic map and decreases on the Poincaré disc. It seems possible to generalize this observation to the phyllotaxis where the size of cells is not constant. Any plane phyllotaxis built using a spiral equation in polar coordinates $(r(s), \theta(s))$ with $\theta(s) = 2\pi s/\tau$ always has the same grain boundaries. Clearly, this applies to composed flowers like sunflowers where the size of florets increases from the core to the periphery due to growth; very similar to the plane representation of the spherical phyllotaxis but with the plane metric.

References

[1] Jean R V 1992 *Five Fold Symmetry* ed I Hargittai (Singapore: World Scientific)
[2] Jean R V 1983 *Math. Biosci.* 64 1–21
[3] Ridley I N 1982 *Math. Biosci.* 58 129–39
[4] Mazrec C and Kappraff J 1983 *J. Theor. Biol.* 103 201–26
[5] Rothen F and Koch A-J 1989 *J. Phys. France* 50 633–57
[6] Rothen F and Koch A-J 1989 *J. Phys. France* 50 1603–21
[7] Rivier N, Koch A J and Rothen F 1991 *Biologically Inspired Physics* ed L Peliti (New York: Plenum) pp 371–80
[8] Rivier N 1992 *J. Phys.: Condens. Matter* 4 913–43
[9] Kappraff J, Blackmore D and Adamson G 1998 *Symmetry in Plants* ed R Jean and D Barabé (Singapore: World Scientific) pp 409–58
[10] Sadoc J-F, Rivier N and Charvolin J 2012 *Acta Crystallogr.* A 68 470–83
[11] Charvolin J and Sadoc J-F 2011 *Biophys. Rev. Lett.* 6 13–27
[12] Dixon R 1992 *Spiral Symmetry* ed I Hargittai and C A Pickover (Singapore: World Scientific)
[13] Hannay J H and Nye J F 2004 *J. Phys. A: Math. Gen.* 37 11591–601
[14] Swinbank R and Purser R J 2006 *Q. J. R. Meteorol. Soc.* 132 1769–93
[15] González A 2010 *Math. Geosci.* 42 49–64
[16] Rivier N, Occelli R, Pantaloni J and Lissowski A 1984 *J. Phys. France* 45 49–63
[17] Rivier N, Miri M F and Oguey C 2005 *Colloids Surf.* A 263 39–45
[18] Rivier N, Sadoc J-F and Charvolin J On the core of phyllotaxy in preparation
[19] Yeatts F R 1997 *Math. Biosci.* 144 71–81
[20] Coxeter H S M 1961 Introduction to Geometry (New York: Wiley)
[21] Rivier N 1988 Mod. Phys. Lett. B 2 195–206
[22] Adler I 1998 J. Algebra 205 227–43
[23] Rivier N 1986 J. Physique Coll. 47 C3-299–309
[24] Hilbert D and Cohn-Vossen S 1952 Geometry and the Imagination (New York: Chelsea)
[25] Thurston W P 2002 The Geometry and Topology of Three-Manifolds chapter 2, Electronic version, www.msri.org/publications/books/gt3m/