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Phyllotaxis, or the properties of spiral lattices.
I. Shape invariance under compression

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Abstract. From the crystallographical point of view, phyllotaxis can be identified with the study of spiral lattices. In this paper, we devote our attention to plane lattices of points. Through a conformal transformation, one gets a lattice of points aligned along a logarithmic spiral. Centuries ago, one recognized the central role the Fibonacci sequence plays in phyllotaxis, as well as the golden ratio $\tau = \frac{1}{2} (1 + \sqrt{5})$: the divergence angle (the angular distance between two consecutive points of the spiral) equals $2 \pi \tau^{-1}$. We define some class of divergence angles more general than the « golden divergence » $2 \pi \tau^{-1}$. This class insures a peculiar shape invariance of the lattice with respect to the change of the plastochrone ratio (or relative rate of growth of the logarithmic spiral).

1. Phyllotaxis.

1.1 Phyllotaxis: A special case of two-dimensional crystallography. — The term phyllotaxis designates the geometry governing the arrangement of the inner florets of a sunflower, of the scales of a pineapple, of the primordia around an apex, and so on. The florets align with spiral whorls in the case of spiral phyllotaxis (sunflower) or with helices in the case of cylindrical phyllotaxis (pineapple or fir-cone).

Figure 1 shows the drawing of a pineapple with hexagonal scales. In this case, the eye is at once drawn towards the spirals which connect neighbouring scales (or cells if one adopts the crystallographic point of view). A given hexagonal (rectangular) cell belongs to three (two)
different such spirals. These spirals are called *parastichies*; they bind each cell with its six (four) neighbours.

Parastichies are grouped into families. We shall discuss this point further in section 3.1, but one can at once get an idea of what is called a *parastichy family*: it is the set of spirals parallel to each other. Figure 1 shows three parastichies going through the hatched scale. Each parastichy is visualized by a full line. The broken line allows us to visualize another parastichy belonging to the same family as that marked with an A. The complete set of parastichies belonging to the same family provides a partition of the whole set of scales into equivalence classes: each scale belongs to a single parastichy of a given family. Moreover, the number $k$ of parastichies belonging to the same family is very important: it alone characterizes the family (see Sect. 3.1).

According to the number of parastichies going through an arbitrary cell, a given perfect (1) phyllotaxis is always particularized by a pair $\{k, l\}$ or a triplet $\{k, l, m\}$ of integers characterizing the two or three families of parastichies occurring throughout the network of cells.

Adler has given a short historical account of the development of phyllotaxis [1] as a scientific discipline. According to his paper, it was recognized very early that $k$, $l$, $m$ are very often successive numbers of the *Fibonacci sequence* $\{f_n\}$

$$\{f_n\} = 1, 1, 2, 3, 5, 8, 13, 21, 34, 55, \ldots$$

(1) We disregard crystallographic defects as dislocations or disclinations.
defined by the recurrence law

\[ f_{k+2} = f_k + f_{k+1} \quad (k \geq 1) \]  

(2)

with

\[ f_1 = f_2 = 1 . \]  

(3)

Moreover, the Fibonacci sequence is related to the golden section \( \tau = \frac{1 + \sqrt{5}}{2} \):

\[ \lim_{n \to \infty} \frac{f_{n+1}}{f_n} = \tau . \]  

(4)

Sometimes, \( \{f_n\} \) is replaced by another sequence called the generalized Fibonacci sequence generated by the same law (2) but with different initial conditions, an example of which is the Lucas sequence \( \{g_n\} \) defined by (2) together with

\[ g_1 = 1 , \quad g_2 = 3 \]  

(5)

so that

\[ \{g_n\} = 1, 3, 4, 7, 11, 18, 29, \ldots \]  

(6)

1.2 THE RELEVANCE OF PHYLLOTAXIS FOR PHYSICAL SCIENCE. — Why do the Fibonacci sequence and, therefore, the golden section, play such an important role in phyllotaxis? There is a long list of well known scientists [1, 3] who were interested by a relation which seems odd at first sight. A great number of these scientists are related to the history of physics, crystallography or mathematics: Kepler [1], Bravais [4], Turing [5], Coxeter [2, 6] or Mackay [7]. According to Adler, Johannes Kepler was the first to assert the relation between the Fibonacci sequence and phyllotaxis (2). Moreover, the Bravais brothers were the first scientists to point out the irrational character of the divergence (for a definition of this term, see Sect. 1.3 and 3.1).

Beside scientists from exact sciences, many biologists of course investigated the same problem and asked the same question. It is very difficult for non-biologists to give a comprehensive review of the biological literature on the subject and our list of references [8-15] is certainly far from being complete.

Finally, other celebrated people [3]: Leonardo da Vinci, Goethe, D’Arcy Thompson, which are difficult to classify in either category mentioned above belong to the history of phyllotaxis.

Quite generally, one can distinguish two broad trends among the scientists who investigated phyllotaxis. The first tendency recruits its partisans rather among physicists, crystallographers or mathematicians. It emphasizes the geometrical character of phyllotaxis and looks for an origin of the arrangement which would also be geometrical. The second tendency, on the other hand, can be found preferably among biologists. It considers the geometrical characteristics of phyllotaxis as an epiphenomenon which has its roots inside the biological cell (3) and which is a consequence of detailed physiological processes. One can mention

(2) The case of Kepler is difficult to classify: one ought perhaps to speak of numerology rather than of mathematics.

(3) Not to be confused with the crystallographical cell which, in our case, identifies itself with the floret of the sunflower or the scale of the pineapple.
Adler's mechanical pressure assumption [1, 11], Venn and Lindenmayer's inhibitor diffusion hypothesis [13] or the assumption of a morphogenetic concentration field [10, 15]. Jean gives a comprehensive review of the various lines of thought on the subject [14].

Of course, these two different points of view are not contradictory but rather complementary. The former one could be called phenomenological and the latter one microscopic. However, the relation between phenomenological and microscopic points of view is not the same in phyllotaxis as in statistical physics for instance. In the latter case, physicists have very general rules allowing them to pass from one level to the other; as a consequence, among physicists, there is some general prejudice, more or less justified, according to which the microscopic level is more important than the phenomenological one.

In the case of phyllotaxis (4), however, there are no automatic rules which allow the phenomenological level to be deduced from the microscopic one. Moreover, if these rules do exist, they have to be discovered in each case and it is not sure that they are independent of the system considered. As a consequence, scientists from exact sciences can be useful in looking for all geometrical characteristics of phyllotaxis. They can emphasize some properties which could be interesting from the biological point of view, even if they cannot analyze the biological causes of these properties.

However this is not the only motivation which can urge physicists to investigate phyllotaxis.

First of all, phyllotaxis belongs to exotic crystallography, but even exotic crystallography is part of crystallography. Next, phyllotaxis makes use of concepts from many domains of physics or crystallography: let us quote for instance scale invariance, inflation or deflation, quasi-periodic lattices, dislocations or disclinations [16]. In the third place, we would mention the physical problems where lattices appear which are similar to those we consider in this paper. This is the case of convective cells moving in the earth's Coriolis field [17]. Another example is the cooling system used in large electromagnets [18]. Last but not least, phyllotaxis is a fascinating subject where elementary (but exotic) plane geometry and elementary properties of continued fractions play a central role. Moreover, as stated above, studying the geometrical model of a botanical pattern does not answer the fundamental question: why? The fact that the biologists do not seem to have given any definite answer still increases the interest of the question, which will no longer be asked in this paper but will always remain in the background of the discussion.

1.3 AIM OF THE PRESENT WORK. — Consider the pineapple of figure 1. Because of the phenomenon of growth, it is possible to order the scales from the bottom to the top of the fruit. In figure 2, the scales have been numbered according to their distance from the bottom (of course, all scales are not visible; their numeration is however easy to simulate).

Let us now suppose that the arrangement of scales is characterized by the three integers {5, 8, 13}. This means that through any scale there goes one parastichy of the five ones belonging to the 5-family, one of the eight ones belonging to the 8-family, and so on for the 13-family (Sect. 1.1). Now, as emphasized above, the n parastichies of the n-family divide the whole set of scales in n disjointed helices (or whorls) which are approximately parallel (n = 5, 8 or 13 here). Hereafter we shall call n-parastichy any parastichy belonging to the n-family.

By construction, each n-parastichy consists of neighbouring scales bearing numbers k, k + n, k + 2 n, ..., where k = 0, 1, 2, ..., n - 1 numbers a given parastichy belonging to the n-family (5). As an immediate consequence, the 5-parastichy going through, say, scale number

(4) We consciously restrict ourselves to this very marginal aspect of structural biology.

(5) The partition of the whole set of scales into the various parastichies of a n-family is nothing but a partition of the natural integers into the classes of residues (mod n).
Fig. 2. — The scales of the pineapple have been numbered from the bottom upward. Notice that the numbers increase regularly along parastichies: from 5 to 5 along parastichies belonging to the same family as A, from 8 to 8 along the family of B and from 13 to 13 along the family of C. One therefore speaks of the 5-family, of the 8-family and so on (Picture drawn according to [2]).

36, consists of scales {..., 26, 31, 36, 41, ...} and is less steep than the 8-parastichy {... 28, 36, 44, ...}. On the other hand, the 13-parastichy {... 23, 36, 49, ...} is even steeper. Moreover, the chirality of the different families alternate: 5-parastichies and 13-parastichies are right-handed whereas 8-parastichies are left-handed.

All these points will be discussed further below (see Sect 3.1 and 3.7) but we are now able to introduce two new definitions. Assimilating the pineapple to a cylinder with circular cross-section, we call (logarithmic) plastochrone ratio the difference of height of two consecutive cells; the height is measured along the axis. On the other hand, we call divergence angle the angular distance between two consecutive cells; in the following, we shall speak merely of divergence which is equal to the divergence angle divided by a factor $2\pi$. Both definitions only make sense if the plastochrone ratio and the divergence are constant. We shall thus define model lattices such that these conditions or equivalent ones are realized (Sect. 3.1).

The difficulty to assimilate the shape of a pineapple or a fir-cone to a cylinder leads directly to the first problem to be dealt with in this paper. Consider the whorl connecting all scales according to their numerical order: 1, 2, 3, ...; this whorl is generally called ontogenic spiral. Now the logarithmic plastochrone ratio can be a constant throughout the network only for a cylinder and for helices with constant pitch. What happens in the case of a pineapple whose shape diverges so much from a cylinder?

In order to answer this question, we proceed as follows. We consider an arbitrary Bravais rectangular point lattice $L_c$ on a cylinder. One can think of $L_c$ as the set of all points aligned along a helix with constant pitch to be identified with the ontogenic spiral; the distance between consecutive points and therefore the divergence are constant (Fig. 3). We then
Fig. 3. — Idealisation of the pineapple. The centres of the scales form a Bravais lattice $L_c$ on the cylinder. They are aligned with a cylindrical helix or ontogenic spiral which connects them in ascending order. A part of this curve is represented by a dotted line on the upper part of the cylinder. The angular distance $2\pi\alpha$ of two consecutive points along it is called divergence angle and their distance along the cylinder axis is the logarithmic plastochrone ratio. The pineapple scales are viewed as Voronoi polygons (see footnote (6)).

investigate how the shape of the Voronoi polygon (6) around each point changes when the cylindrical lattice $L_c$ is uniformly compressed (or dilated) along the symmetry axis of the cylinder, the divergence being fixed. When such a compression occurs, the lattice is steadily distorted. During this process, however, points $Q_1$, $Q_2$, ... which were nearest neighbours of a given point $P$ no longer remain nearest to $P$: new points come from above which approach closer to $P$. The Voronoi polygon around $P$ being determinated by the location of the (in general) six nearest neighbours of $P$ changes discontinuously when a change of neighbours occurs.

There are two consequences of this change:

A. There is a parastichy transition. If $k$ and $l$ were the former parastichy numbers, they are replaced by a new couple, say $k'$ and $l'$ ($k'$ and $l'$ need not to be both different from $k$ and $l$)

$$
\{k, l\} \rightarrow \{k', l'\} \\
k' = F_1(k, l) \quad l' = F_2(k, l) .
$$

(6) The Voronoi polygon (or Wigner-Seitz cell, or Dirichlet domain) is the set of all points (here, of the cylinder) which are nearer to a given element of a discrete point-lattice than to any other element.
The actual value of the divergence will be determined by $F_1$ and $F_2$. We shall find that the shape of the Voronoi polygon changes the least when the divergence is equal to the golden section ($\tau$).

B. When the lattice undergoes a sequence of parastichy transitions, there is a series of oscillations of the shape of the Voronoi polygon around a mean shape. Meanwhile the size of the cell decreases continuously because we obviously consider the points of the lattice as indiscernible. Figure 4 shows the result of such parastichy transitions on the shape and the size of the Voronoi polygon.

The same result is valid for the case of plane phyllotaxis where points of the plane lattice align with a logarithmic spiral (Fig. 6b), the divergence angle being now defined as the angle between the radius-vectors from the center of the spiral to two consecutive points. We call \textit{spiral lattice $L_s$} the lattice thus constructed. In this case, the plastochrone ratio $z > 1$ is the ratio of the distances of two consecutive points to the center O of the spiral (see Sect. 3.1).

No doubt that this result, rather easy to obtain, is important for botany. The spiral lattice of plane phyllotaxis is an idealized model of a daisy or a sunflower. However, it can also be

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(7) More precisely, to $\tau - 1 = \tau^{-1}$ because the angles $2\pi\tau$ and $2\pi(\tau - 1)$ are obvious equivalent.
considered as the idealized projection of the scale arrangement of a pineapple on a plane perpendicular to the symmetry axis. As a consequence, the approximate invariance of the Voronoi polygon strongly suggests the following fact. Take any arrangement of botanical units (florets, scales) on an ontogenic spiral running on a surface of revolution. Just require that the divergence shall be constant and equal to the golden section: the geometrical neighbourhood will be almost the same for all units and their shapes will be preserved along the spiral. Only their orientation and size will vary from place to place.

We can now answer the question asked above. In real systems such as daisies or sunflowers where the plastochrone ratio cannot be considered as constant but seems to decrease as one goes away from the center, there are domains (in general concentric rings). Each of them is characterized by a local couple of parastichy numbers \( \{k, l\} \). From one domain to the next, a parastichy transition occurs. This transition is identified as a circular defect line. These defects have been studied by Rivier [16] and Käppeli [19] who emphasized their quasi-crystalline structure. On the other hand, if the divergence equals the golden section and remains constant throughout the pattern, the shape invariance of the botanical cells is everywhere preserved.

In a forthcoming paper [20], hereafter identified as II, we shall consider the spiral lattice \( L_s \) just mentioned above. Taking for granted that the « best » divergence is equal to the golden section (golden divergence), we shall ask the following question: is there a growth mechanism of geometrical nature which can explain the emergence of the golden divergence among plants?

1.4 PLAN OF THE PRESENT PAPER. — In part 2, we shall recall some properties of continued fractions to be used in the present paper or in II. The results are merely stated without demonstration but the material we shall use essentially belongs to the very beginning of the literature on the subject [21, 22].

Part 3 contains the main topics of the paper. The concepts of principal and intermediate neighbours of a point are introduced and coupled to those of principal and intermediate convergents of the divergence, the latter concepts deriving from the development of the divergence as a continued fraction. Later, nearest neighbours and principal as well as intermediate neighbours are identified. Parastichy transitions, and specially standard parastichy transitions are defined and the conditions for shape invariance under a standard transition are established. « Translation invariant » continued fractions are shown to correspond to shape invariance of the lattice.

In part 4 we discuss the predominant role played by the golden divergence among translation invariant continued fractions. Eventually the relevance of the given arguments for plants is shortly discussed.

2. Continued fractions.

2.1 CONTINUED FRACTIONS AND PRINCIPAL CONVERGENTS. — Let us consider the finite or infinite sequence \([a_1, a_2, a_3, \ldots]\) of positive integers \(a_i\), \((i = 1, 2, 3, \ldots)\); it defines a continued fraction \(x\)

\[
x = \cfrac{1}{a_1 + \cfrac{1}{a_2 + \cfrac{1}{a_3 + \cdots}}} = [a_1, a_2, a_3, \ldots].
\]
The process defined by (8) always converges to a real number $0 < x \leq 1$. The sequence of rational fractions

$$\frac{p_1}{q_1} = \frac{1}{a_1} = [a_1] \quad \frac{p_2}{q_2} = \frac{1}{a_1 + \frac{1}{a_2}} = [a_1, a_2]$$

$$\frac{p_3}{q_3} = [a_1, a_2, a_3] \quad \frac{p_n}{q_n} = [a_1, a_2, \ldots, a_n]$$

is finite if $x$ is rational, infinite in the opposite case. The fractions $\frac{p_n}{q_n}$ $(n = 1, 2, \ldots)$ are the successive principal convergents (PC) of $x$. They satisfy

$$p_{n+2} = a_{n+2} p_{n+1} + p_n \quad (n \geq 0)$$

$$q_{n+2} = a_{n+2} q_{n+1} + q_n$$

with

$$p_0 = 0 \quad p_1 = 1$$

$$q_0 = 1 \quad q_1 = a_1$$

We summarize below properties of principal convergents we shall use. Their demonstration can be found in the well known books by Khinchine [21] or Lang [22].

A. $q_n$ and $q_{n+1}$ are relatively prime for all $n \geq 1$.

B. Numerators and denominators of two successive principal convergents satisfy

$$q_{n+1} p_n - p_{n+1} q_n = (-1)^{n+1}.$$  \(12\)

C. Even-order convergents form an increasing sequence and odd-order convergents, a decreasing sequence. Every odd-order convergent is greater than any even-order convergent. If the continued fraction is infinite ($x$ is then irrational)

$$\begin{cases} 
\frac{p_n}{q_n} \leq x & (n \text{ even}) \\
\frac{p_n}{q_n} \geq x & (n \text{ odd}). 
\end{cases}$$  \(13\)

D. Given a rational number $x = [a_1, a_2, a_3, \ldots, a_{n+1}]$, one defines a function $x(y)$ by

$$x(y) = [a_1, a_2, a_3, \ldots, a_{n+1}, 1/y] \quad 0 < y \leq 1.$$  \(14\)

This function can be expressed as

$$x(y) = \frac{p_{n+1} + p_n y}{q_{n+1} + q_n y}.$$  \(15\)

Using (12), one shows that

$$\frac{dx(y)}{dy} = \frac{(-1)^{n+1}}{(q_{n+1} + q_n y)^2} \quad \begin{cases} > 0 & \text{if } n \text{ is odd} \\ < 0 & \text{if } n \text{ is even}. \end{cases}$$  \(16\)
E. If \( p_n/q_n \) and \( p_{n+1}/q_{n+1} \) are principal convergents of \( x \), the following inequalities hold

\[
\left\{ \begin{array}{c}
\frac{1}{2q_{n+1}} < |q_n x - p_n| < \frac{1}{q_{n+1}} \\
|q_n x - p_n| < \frac{1}{2q_n}
\end{array} \right.
\] (17)

F. If \( 0 < x < 1 \) satisfies an irreductible algebraic equation of 2nd degree with rational coefficients, \( x \) is said to be a quadratic irrational. In this case, the continued fraction representing \( x \) is said to be periodic:

\[
x = [a_1, a_2, \ldots, a_r, a_{r+1}, \ldots, a_{r+s}, a_{r+1}, \ldots] =
\equiv [a_1, a_2, \ldots, \overline{a_{r+1}, \ldots, a_{r+s}}].
\] (18)

This writing means that the coefficients \( a_k \) form a periodic sequence of length \( s > 1 \) from the \((r + 1)\)th item of the development.

G. Given \( x = [a_1, a_2, a_3, \ldots] \) such that \( 0 < x < 1/2 \) (this implies \( a_1 > 1 \)), one easily checks that \( 1 - x \) is equal to

\[
1 - x = [1, a_1 - 1, a_2, a_3, \ldots].
\] (19)

2.2 INTERMEDIATE CONVERGENTS. — Let us consider the representation (8) of the real number \( 0 < x < 1 \). If \( a_{k+2} > 1 \) for some \( k \geq 0 \), we can build the following rational fractions

\[
\frac{p_k}{q_k}, \frac{p_k + p_{k+1}}{q_k + q_{k+1}}, \frac{p_k + 2p_{k+1}}{q_k + 2q_{k+1}}, \ldots, \frac{p_k + a_{k+2}p_{k+1}}{q_k + a_{k+2}q_{k+1}} = \frac{p_{k+2}}{q_{k+2}}.
\] (20)

This series of fractions form, for even \( k \), an increasing sequence and, for odd \( k \), a decreasing sequence. Those fractions which have the form \( \frac{p_k + rp_{k+1}}{q_k + rq_{k+1}} \), with \( r \) integer in the range \( 0 < r < a_{k+2} \), are called intermediate convergents (IC). In order to state a property common to principal and intermediate convergents, we have to give a definition.

A best rational approximation of a real number \( 0 < x < 1 \) is a rational fraction \( a/b \) such that

\[
\left| x - \frac{p}{q} \right| < \left| x - \frac{a}{b} \right|
\] (21)

for \( p, q \) integers implies \( q > b \). In other words, \( a/b \) is the best rational approximation of \( x \) if all rational fractions with denominator \( q \leq b \) differ more from \( x \) than \( a/b \) itself. We can now state property H (*)

H. Every best approximation of a number \( 0 < x < 1 \) is a principal or an intermediate convergent of the continued fraction representing this number.

(*) For this property to have no exception, one should define also convergent \( \frac{p - 1}{q - 1} \) [21]. However, this is of no importance here.
3. Shape invariance in a phyllotaxis with golden divergence.

3.1 RELATION BETWEEN CYLINDRICAL AND SPIRAL LATTICES. — Let us consider the complex Euclidean plane \( w = u + iv \). The points

\[ w_{n,m} = u_{n,m} + iv_n = (-\alpha + i\beta)n + m \]  

form a lattice we call the extended cylindrical lattice \( L_L \). \( \alpha \) and \( \beta \) are arbitrary real numbers while both \( n \) and \( m \) run over the whole set of integers. From \( L_L \), we can easily build the cylindrical and the spiral lattices introduced in section 1.3.

A. If \( \alpha \) is irrational, the sublattice of \( L_L \) built from the points \( w_{n,m} \) such that \( 0 \leq u_{n,m} < 1 \) is isomorphic to the cylindrical lattice \( L_c \). The divergence and the logarithmic plastochrone ratio are equal to \( \alpha \) and \( \beta \) respectively. In the following, barring any indication to the contrary, we shall not distinguish between \( L_c \) and \( L_L \).

B. If we look at figure 5, we see a finite part of an extended cylindrical lattice. The points there are identified merely by the value of the integer \( n \) from (22). We see that a sequence of contiguous points on a straight line are numbered as an arithmetic progression whose increment

![Figure 5](image-url)

Fig. 5. — A part of an extended lattice \( L_L \) is represented here. This picture is drawn with \( \alpha = \sqrt{2} - 1 = [2] \). Points are located at coordinates \((u_{n,m}, v_n) = (-\alpha n + m, \beta n)\); they are distinguished by the mere value of \( n \). A Voronoi polygon is drawn around the origin: it encloses all points of the \((u, v)\)-plane nearer to 0 than to any other point of the lattice \( L_L \). \( P_+ (P_-) \) is the convex envelope of all points of the lattice located above 0 on the right (left) of the axis \( u = 0 \). Its vertices are the principal neighbours of the origin (so are points 2, 12, ... on \( P_+ \) and 5, 29, ... on \( P_- \)). Between principal neighbours are (possibly) located intermediate neighbours of 0 (here points 7, 17, 41, ...).
is equal to the parastichy number (the image of a straight line of $L_L$ is a spiral on the spiral lattice $L_s$ (see (23)) and a helix on the cylindrical lattice $L_c$). For instance, points (..., 0, 5, 10, 15, ...) and (..., 1, 6, 11, 16, ...) belong to the 5-family of parastichies while (..., 1, 8, 15, 22, ...) belong to the 7-family.

C. The conformal transformation

$$Z = X + iY = e^{-i \frac{\pi}{2} u} = e^{-i \frac{\pi}{2} (u + iv)}$$  \hspace{1cm} (23)

maps the strip $0 \leq u < 1$ onto the whole complex plane. The image of $L_c$ through (23) is given by the set

$$Z_n = e^{-i \frac{\pi}{2} n(-\alpha + i\beta)} = R_n e^{i\phi_n}$$  \hspace{1cm} (24)

with $R_n = e^{2\pi n\beta}$ and $\phi_n = 2\pi n\alpha$ which constitutes the spiral lattice $L_s$ mentioned above (Sect. 1.3 and Fig. 6b). All these points align with the logarithmic spiral, specified with the help of polar coordinates $(R, \phi)$

$$R = e^{(\beta / \alpha)} \phi.$$  \hspace{1cm} (25)

The plastochrone ratio $z$ is related to the logarithmic plastochrone ratio $\beta$ by

$$z = \frac{R_{n+1}}{R_n} = e^{2\pi \beta}$$  \hspace{1cm} (26)

and the divergence $x$ corresponds to the same definition as for $L_c$:

$$x = \frac{\phi_{n+1} - \phi_n}{2\pi} = \alpha$$  \hspace{1cm} (27)

so that, without loss of generality, we assume $0 < x < 1$. Figure 6 shows the relation between the various point lattices introduced so far and one of their common source, the pineapple fruit!

The lattice $L_s$ is self-similar, as noticed in section 1.3. As a special case, the neighbourhoods of two arbitrary points of $L_s$ are similar: they can be made identical by the product of a rotation and a scale transformation. We shall use this property in the next section.

3.2 Shape invariance of a Voronoi polygon around a lattice point. — We are interested to study the shape invariance of the neighbourhood of an arbitrary point of the lattice $L_L$ when the plastochrone ratio $\beta$ changes, the divergence $\alpha$ being hold constant. We can make two important remarks.

A. If $\alpha$ is rational, there cannot exist such shape invariance [17]. As a matter of fact, consider figure 7. Due to the rational value of $\alpha$, there are infinitely many points of $L_L$ located exactly above each point, including the origin 0. As a consequence, if we decrease $^9 \beta$, all points situated on the same vertical as 0 will eventually come arbitrarily close to it, unlike the other points of the lattice which will remain at a finite distance of the origin.

B. Due to the self-similarity of $L_s$, the invariance of the shape of the neighbourhood of any point of $L_L$ is automatically transposed to $L_s$. As a consequence, we shall restrict ourselves to the discussion of $L_L$.

In order to test the shape invariance of the neighbourhood of a point of $L_L$, we shall first take advantage of the translation symmetry of $L_L$ and consider the neighbourhood of the

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(9) In the following, we shall always reduce $\beta$ in order to simplify the discussion, but we could increase it as well.
Fig. 6. — The pineapple (a) is idealized as a cylinder (c) on this lattice $L_c$, each point represents the center of a pineapple scale. Unrolling the cylinder on a plane, one gets the extended lattice $L_L(d)$. The spiral lattice $L_s(b)$ is obtained from $L_L$ by the conformal transformation $X + iY = e^{-i\pi/2}(u + iv)$, where $(u, v)$ are the coordinates of a point in the plane of $L_L$ and $(X, Y)$ those of the image point in the plane of $L_s$. Due to this transformation, the divergence $\alpha$ and the logarithmic plastochrone ratio $\beta$ are replaced, in $L_s$, by $x = \alpha$ and $z = e^{2\pi} \beta$ respectively. In $L_L$, $2\pi\alpha$ is the angular distance of two consecutive points along the ontogenic spiral; $z$ is the ratio of their respective distance to the center of the spiral.

How can this shape invariance be tested? Taking still advantage of the translation symmetry, we shall draw our attention toward the behaviour of the Voronoi polygon (VP) encircling the origin 0 (for a definition of VP, see the footnote (6)). If we decrease $\beta$ by a large amount, all points of $L_L$ located above the axis $v = 0$ move downward along a vertical. During this process, points which were, at the beginning, nearest neighbours of the origin are stepwise replaced by other points. Now the nearest neighbours of 0 do determine the shape of the VP (see next Sect.). Strict shape invariance of the VP is therefore impossible: during the steady reduction of $\beta$, the VP distorts little by little. When one of the nearest neighbours is replaced by another point, the shape of the VP changes discontinuously. In a real lattice, there is some interaction between the sites (if they are occupied by scales or florets, there is some mechanical constraints between the neighbouring cells), so that one can speak of an equilibrium configuration corresponding to a given set of nearest neighbours. When this set is partially or wholly replaced by a new one, the latter defines a new configurational equilibrium. What we demand is that the geometry of two local configurations separated by a
If the divergence $\alpha$ is rational (here $\alpha = 1/3$), the points of the lattice $L_l$ align with vertical lines. As can be seen, there is no shape invariance of the Voronoi polygon when the logarithmic plastochrone ratio $\beta$ is reduced, i.e. when the lattice is compressed along the vertical direction. Dashed lines indicate two of the most visible parastichies.

### 3.3 Nearest Neighbours of a Lattice Point

The construction of a Voronoi polygon around a lattice-point 0 is well known: draw a segment $S_Q$ of straight line connecting 0 with each neighbour $Q$ of 0. For all $Q$, cut $S_Q$ in the middle by a perpendicular $d_Q$. The interior envelope $E$ of all $d_Q$ encloses the VP around 0 (see Fig. 5). Now $E$ consists of a finite number (here six) of segments $d_{Q_1}$, say $d_{Q_1}, d_{Q_2}, \ldots, d_{Q_6}$. The six corresponding points $Q_i$ ($i = 1, \ldots, 6$) are the nearest neighbours of the origin. As emphasized above, we are merely interested in the three points (say $Q_1, Q_2, Q_3$) which lie above 0 and to which we shall reserve the name of nearest neighbours (NN) in the future.

How do we test the shape invariance of the VP when point $Q_i$ is replaced as a NN by $Q'_i$ ($i = 1, 2, 3$)? We say that points $Q'_i$ define a neighbourhood similar to that which corresponds to the set $Q_i$ if

$$\frac{u_1(\beta')}{u_1(\beta)} = \frac{u_2(\beta')}{u_2(\beta)} = \frac{u_3(\beta')}{u_3(\beta)},$$

$$\frac{v_1(\beta')}{v_1(\beta)} = \frac{v_2(\beta')}{v_2(\beta)} = \frac{v_3(\beta')}{v_3(\beta)}$$

(28)

where $(u_i(\beta), v_i(\beta))$ are the coordinates of $Q_i$ for a given value of $\beta$. Now, according to (22), $u_i$ does not depend on $\beta$ while $v_i$ is merely proportional to $\beta$. We can therefore rewrite (28) as

$$\frac{u_1'}{u_1} = \frac{u_2'}{u_2} = \frac{u_3'}{u_3}$$

$$\frac{v_1'}{v_1} = \frac{v_2'}{v_2} = \frac{v_3'}{v_3}$$

(29)

without further specification of $\beta$. 

---

Fig. 7. — If the divergence $\alpha$ is rational (here $\alpha = 1/3$), the points of the lattice $L_l$ align with vertical lines. As can be seen, there is no shape invariance of the Voronoi polygon when the logarithmic plastochrone ratio $\beta$ is reduced, i.e. when the lattice is compressed along the vertical direction. Dashed lines indicate two of the most visible parastichies.
In order to use equation (29), we have to determine what are the NN of the origin for a given $\beta$. This is done in the next section.

3.4 PRINCIPAL AND INTERMEDIATE NEIGHBOURS OF A LATTICE POINT. — To this aim, we use a variant of a construction of Klein [14] which is due to Coxeter [23].

Draw $P_+$ ($P_-$), the convex envelope of all points of $L_L$ located above 0 and on the right (left) of the imaginary axis ($u = 0$, $v > 0$). Because $\alpha$ is irrational, $P_+$ and $P_-$ are semi-infinite polygons whose vertices are called the principal neighbours (PN) of the origin. Moreover, $P_+$ and $P_-$ meet the intermediate neighbours (IN) of 0 which are located on a segment joining two PN situated on the same side of the imaginary axis (see Fig. 5).

All vertices of $P_+$ and $P_-$ satisfy

\[
\begin{align*}
    u_{n,m}(P_+) &= \lfloor \alpha n \rfloor - \alpha n + 1 = u_n(P_+) \\
    u_{n',m'}(P_-) &= \lfloor \alpha n' \rfloor - \alpha n' = u_n(P_-).
\end{align*}
\]  

$[\alpha]$ is the greatest integer smaller or equal to the real number $\alpha$. Notice that the coordinates (30) only depend on the integer $n(n')$ which therefore allows us to distinguish between all points $H$ of $L_L$ belonging to $P_{\pm}$.

According to the definition of PN and IN, there is a one-to-one correspondence between PN and the principal convergents of the divergence $\alpha$ on one hand, between IN and its intermediate convergents on the other hand [23]. This correspondence takes the following form:

A. In the case of a PN with coordinates $(u_n(P_\pm), v_n(P_\pm))$ and corresponding to the $k$-th principal convergent (PC), we write:

\[
\begin{align*}
    u_{n_k}(P_+) &= \lfloor \alpha n_k \rfloor - \alpha n_k + 1 = p_k - \alpha q_k \\
    v_{n_k}(P_+) &= \beta n_k = \beta q_k \\
    u_{n_k}(P_-) &= \lfloor \alpha n_k \rfloor - \alpha n_k = p_k - \alpha q_k \\
    v_{n_k}(P_-) &= \beta n_k = \beta q_k
\end{align*}
\]  

$k$ odd.

B. For an IN with coordinates $(u_n(P_\pm), v_n(P_\pm))$ and located between the $k$-th and the $(k + 2)$-th PN at the $r$-th place, one gets

\[
\begin{align*}
    u_{n_k,r}(P_+) &= \lfloor \alpha n_{k,r} \rfloor - \alpha n_{k,r} + 1 \\
    &= (p_k + r p_{k+1}) - \alpha (q_k + r q_{k+1}) \\
    v_{n_k,r}(P_+) &= \beta n_{k,r} = \beta (q_k + r q_{k+1}) \\
    u_{n_k,r}(P_-) &= \lfloor \alpha n_{k,r} \rfloor - \alpha n_{k,r} \\
    &= (p_k + r p_{k+1}) - \alpha (q_k + r q_{k+1}) \\
    v_{n_k,r}(P_-) &= \beta n_{k,r} = \beta (q_k + r q_{k+1})
\end{align*}
\]  

$k$ even.

Notice that $n_{k,0} = n_k$ and $n_{k,a_{k+2}} = n_{k+2}$, as it should be, so that (31) is merely a special case of (32). Moreover, (32) shows that any principal or intermediate neighbour can be unambiguously specified by the couple $(k, r)$ with $0 \leq r < a_{k+2}$. 
3.5 Nearest Neighbours are either Principal or Intermediate Neighbours. — We now state two important but almost obvious rules:

3.5.1 Nearest neighbours are either principal or intermediate neighbours. — This statement should be obvious if one looks at figure 5. Let us namely consider a point of the lattice not lying on \( P_\pm \). There are two situations if we restrict our consideration to the points immediately behind \( P_\pm \). In the first case, this point (say \( Q_1 \)) lies on the straight line joining \( O \) to a point \( P_2 \) of \( P_\pm \): look at point 14 behind 7 (10). In the second situation, the point considered \( Q_2 \) forms a rhomb with \( O \) and two consecutive points \( P_2 \) and \( P_3 \) of \( P_+ \) or \( P_- \): as an example, take \((0, 7, 12, 19)\).

In the former case \( Q_1 \) is obviously not a nearest neighbour. In the latter case, the conclusion is the same: let us call \( d_{Q_2} \) the perpendicular to \( OQ_2 \), bisecting this segment; \( d_{Q_2} \) cuts the line \( OQ_2 \) on \( P_\pm \) and at least one of the points \( P_2 \), \( P_3 \) is on \( d_{Q_2} \) or nearer to \( O \) than \( d_{Q_2} \) itself.

3.5.2 In the upper half of \( L_+ \), the nearest point to the origin \( O \) is always a principal neighbour. — The proof can also be given with the help of figure 5. Let us consider point 7, which is an IN of \( O \). Being located between points 2 (PN of rank 1) and 12 (PN of rank 3), 7 forms with 0, 5 (PN of rank 2) and 12 a rhomb. Now, by construction, \( |u_7| = |u_5| + |u_12| \) and \( v_7/v_5 = 7/5 > 1 \), so that distance \( 05 < \text{distance } 07 \). This result is quite general, as the proof obviously does not depend on the choice of point 7 as IN.

As a consequence, we can restate rule 1: Nearest neighbours are either principal or intermediate neighbours; at least one of them is principal.

Let us call nearest neighbour transition (NNT) a finite reduction of the plastochrone ratio \( \beta \) leading to a change in the set \( \{Q\} \) of NN. We are then in a position to discuss such a NNT from the point of view of the shape invariance of the VP.

3.6 Shape Invariance of the VP through a Nearest Neighbour Transition. — Let us consider two triplets of points, namely \( \{Q\} = \{Q_1, Q_2, Q_3\} \) and \( \{Q'\} = \{Q'_1, Q'_2, Q'_3\} \). For a given value \( B'(B') \) of the plastochrone ratio, \( \{Q\} (\{Q'\}) \) is the set of NN of the origin. We consider the NNT \( (\beta \rightarrow \beta') \). As noticed in section 3.3, this transition leads to the shape invariance of the VP if their coordinates \((u, v_i)\) and \((u', v'_i)\) satisfy equation (29) which we rewrite somewhat more explicitly

\[
\frac{u'_1}{u_1} = \frac{u'_2}{u_2} = \frac{u'_3}{u_3} = \kappa
\]

\[
\frac{v'_1}{v_1} = \frac{v'_2}{v_2} = \frac{v'_3}{v_3} = \kappa'
\]

where \( \kappa \) and \( \kappa' \) are nothing but the common values of the two sets of ratios.

In order to avoid unnecessary tedious calculations, we make from the beginning an assumption on the form of \( \{Q'\} \). We assume that the transition which could preserve the shape of the VP replaces each NN of \( \{Q\} \) by an element of \( \{Q'\} \) in such a way that a point \((k, r)\) is replaced by \((k + 1, r)\). We call standard transition such a transition. We show below that in general a transition which is not standard cannot preserve the shape invariance.

\((10)\) In figure 5, points are specified with the mere help of the integer \( n \) from relation (22), while integer \( m \) is omitted, which should lead to no confusion.
In order to visualize these concepts, let us look at the VP represented on figure 5 where points 2, 5 and 7 are NN. Through a standard transition we meet points 5, 12, 17 (Tab. I).

<table>
<thead>
<tr>
<th>Before transition</th>
<th>After transition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nearest neighbour</td>
<td>k</td>
</tr>
<tr>
<td>(Q₁)</td>
<td>2</td>
</tr>
<tr>
<td>(Q₂)</td>
<td>5</td>
</tr>
<tr>
<td>(Q₃)</td>
<td>7</td>
</tr>
</tbody>
</table>

On the other hand, there is another set \( \{Q''\} = \{Q₁', Q₂', Q₃'\} \) which can represent the NN of the origin for some values of \( \beta \) (Tab. II).

<table>
<thead>
<tr>
<th>Nearest neighbour</th>
<th>k</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Q₁')</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>(Q₂')</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>(Q₃')</td>
<td>12</td>
<td>3</td>
</tr>
</tbody>
</table>

Obviously, the ratios of the coordinates of \( \{Q\} \) and \( \{Q''\} \) cannot satisfy the condition of shape invariance (33). Moreover no standard transition can relate \( \{Q\} \) and \( \{Q''\} \).

Let us look for the shape invariance with respect to the standard transition. According to (32) and (33) we have to compute

\[
\frac{u_{nk+1,r}}{u_{nk,r}} = \frac{(p_{k+1} + r p_{k+2}) - \alpha (q_{k+1} + r q_{k+2})}{(p_{k} + r p_{k+1}) - \alpha (q_{k} + r q_{k+1})}
\]

which makes sense for \( 0 \leq r < \inf (a_{k+2}, a_{k+3}) \). Here \( \inf (x, y) \) is defined by

\[
\inf (x, y) = \begin{cases} x & \text{if } x \leq y \\ y & \text{if } x \geq y \end{cases}
\]

Making use of the recursion relation (10), we can write (34) as

\[
\frac{u_{nk+1,r}}{u_{nk,r}} = \lambda_{k,r} + \frac{u_{nk-1,r}}{u_{nk,r}}
\]

where

\[
\lambda_{k,r} = a_{k+1} \frac{1 + r \frac{a_{k+2} p_{k+1} - \alpha q_{k+1}}{a_{k+1} p_k - \alpha q_k}}{1 + r \frac{p_{k+1} - \alpha q_{k+1}}{p_k - \alpha q_k}}
\]
Fig. 8. — \( \alpha \) is a noble number (here \( \alpha = \tau^{-1} = [1] \)); decreasing the logarithmic plastochrone ratio \( \beta \) only leads to standard parastichy transitions. a) Parastichies belong to the 2- and 3-families (respectively left and right handed). b) The lattice of (a) is compressed along the vertical direction (by mere decrease of \( \beta \)). A parastichy transition occurs: parastichies now belong to the 3- and 5-families. c) Further decreasing \( \beta \) leads to another transition: now 5- and 8-families are visible. Notice how the shape of the Voronoi polygon is preserved; only its size and orientation vary.

(36) and (37) make sense only if \( r < a_{k+1} \) so that one can summarize the conditions on \( r \) as

\[
0 \leq r < \inf (a_{k+1}, a_{k+2}, a_{k+3}).
\]  

(38)

Relation (36) can be used in particular cases to test the shape invariance of a unique transition. However it is easier to work out if we consider a special class of divergences. Let us assume that all coefficients \( a_k \) of the development of the divergence as a continued fraction are equal:

\[
a_k = a \quad \text{for all } k.
\]  

(39)

\( a \) is some positive integer. Relation (39) implies

\[
\alpha = \frac{1}{a + \frac{1}{\frac{1}{a + \cdots}}} = [a, a, \ldots] = [\overline{a}] = -a + \sqrt{a^2 + 4} \over{2}
\]  

(40)

where the same notation as is equation (18) has been used. As a consequence, \( \lambda_{k, r} \) no longer depends on \( (k, r) \) and (36) reads

\[
\frac{u_{nk+1, r}}{u_{nk, r}} = a + \frac{u_{nk-1, r}}{u_{nk, r}}.
\]  

(41)

In order to determine \( \frac{u_{nk+1, r}}{u_{nk, r}} \), let us define

\[
\phi_{k, r} = -\frac{u_{nk+1, r}}{u_{nk, r}} > 0.
\]  

(42)
The fact that $\phi_{k,r} > 0$ is the direct consequence of statement C of section 2.1. Now we first notice that if we call

$$\phi_\infty = \lim_{k \to \infty} \phi_{k,r}$$

equation (41) then becomes

$$\phi_\infty = \phi_\infty^{-1} - a$$

whose positive solution $\phi_\infty^+$, reads

$$\phi_\infty^+ = -a + \sqrt{a^2 + 4 \over 2} = \alpha .$$

We show in Appendix that this result is valid for all values of $k$:

$$\phi_{k,r} = -a + \sqrt{a^2 + 4 \over 2} = \alpha$$

so that the first part of (33) is automatically satisfied. We still have to check whether the second part is also true. We then have to evaluate $v_{n_k+1,r}^{n_k,r}$ with the help of (32):

$$v_{n_k+1,r}^{n_k,r} = \frac{q_{k+1} + rq_k + 2}{q_k + r q_{k+1}} .$$

For convenience, we shall hereafter evaluate the inverse of $v_i'$ from equation (33). Because of (9-11) and (40), it follows that

$$\frac{q_k}{q_{k+1}} = \frac{p_k + 1}{q_{k+1}} = [a, a, \ldots, a] \quad (a \text{ occurs } k + 1 \text{ times}) .$$

For $r = 0$,

$$v_{n_k,0}^{n_k+1,0} = \frac{p_k + 1}{q_{k+1}}$$

while for $r = a$

$$v_{n_k,a}^{n_k+1,a} = \frac{p_k + 3}{q_{k+3}} .$$

Now (16) shows that $v_{n_k,r}^{n_k+1,r}$ is a monotonic function of $r$ in the interval considered. As a consequence

$$\alpha < \frac{v_{n_k,r}^{n_k+1,r}}{p_k + 1} \leq \frac{q_{k+1}}{q_{k+1}} \quad k \text{ even}$$

$$\alpha > \frac{v_{n_k,r}^{n_k+1,r}}{p_k + 1} \geq \frac{q_{k+1}}{q_{k+1}} \quad k \text{ odd} .$$
As a conclusion, we can say that the invariance of the VP is almost realized during a standard transition. As a matter of fact, (51) shows that, in general, \( \frac{v_i^j}{v_i} \) cannot be strictly equal for all values of \( i (i = 1, 2, 3) \) because it slightly depends on \( k \) and \( r \). Now (17) and (51) show that this dependence will strongly decrease with increasing \( k \).

3.7 PARASTICHY TRANSITIONS. — Any exchange \((k, r) \rightarrow (k', r')\) corresponds to a parastichy transition. As a matter of fact, the couple \((k, r)\) which identifies one of the nearest neighbours also shows that points 0 and \( q_k + rq_{k+1} \) are contiguous on a straight line \( (q_k + rq_{k+1} \) is the actual value of the integer \( n \) in (22) which corresponds to \((k, r))\). Moreover, parastichies are those straight lines of \( L_L \) which bind neighbouring points (see also Sect. 1.3 and 3.1).

Table III summarizes the correspondences between two concepts: nearest neighbours on the one hand and parastichy families on the other hand.

<table>
<thead>
<tr>
<th>Nearest neighbours</th>
<th>Parastichy families</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nearest neighbour ((k, r))</td>
<td>Parastichy family ( n = q_k + rq_{k+1} )</td>
</tr>
<tr>
<td>Nearest neighbour transition ((k, r) \rightarrow (k', r'))</td>
<td>Parastichy transition ((q_k + rq_{k+1}))-family</td>
</tr>
<tr>
<td>Standard transition ((k, r) \rightarrow (k + 1, r))</td>
<td>Standard parastichy transition ((q_k + rq_{k+1}))-family</td>
</tr>
</tbody>
</table>

Notice an important point: the chirality (or sense of whirling) of a parastichy is fixed by the parity of the number \( k \). This is a consequence of the fact that principal convergents of a divergence alternate above and below its value (Sect. 2.1).

3.8 RATE OF SIZE REDUCTION DURING A STANDARD TRANSITION. — From equation (32), we know that \( v_{nk,r}(\beta) \) depends on the plastochrone ratio according to

\[
v_{nk,r}(\beta) = \beta (q_k + rq_{k+1}) .
\]

Let us consider a standard transition \((k, r) \rightarrow (k + 1, r)\) during which \( \beta \rightarrow \beta' \). What is the ratio \( \beta'/\beta \) which insures shape invariance?

The answer is very simple. \( \beta' \) must be such that

\[
\frac{v_{nk+1,r}(\beta')}{v_{nk,r}(\beta)} \equiv \left| \frac{u_{nk+1,r}}{u_{nk,r}} \right| = \alpha .
\]

We again find a value of \( \beta'/\beta \) depending slightly on \((k, r)\) but we ignore this dependence, being merely interested in the order of magnitude of \( \beta'/\beta \).
Because of (51-53), we get
\[
\frac{q_{k+1} + rq_{k+2}}{q_k + rq_{k+1}} \frac{\beta'}{\beta} \approx \alpha^{-1} \frac{\beta'}{\beta} = \alpha
\]
so that
\[
\beta'/\beta \approx \alpha^2.
\]
The ratio \( R_L \) of the linear dimensions of the VP after and before the transition is simply given by
\[
R_L \approx \left| \frac{u_{nk+1,r}}{u_{nk,r}} \right| = \alpha.
\]
This result is quite natural: we get a shape invariance of the crystallographic cell (here the VP) by compressing the lattice in only one direction. This compression alone must « absorb » the whole size reduction, as clearly shown from equations (55) and (56).

3.9 Generalization to a Larger Class of Divergences. — In the preceding sections, we restricted our consideration to the parastichy transitions corresponding to a reduction of the parameter \( \beta \). We shall keep the same point of view while showing that a larger class of divergences preserves the shape invariance of the VP around a point — and therefore the whole lattice.

For this purpose, consider the irrational numbers \( \alpha' \) given by the following development
\[
\alpha' = [a_1', ..., a_m', a, a, a, ...] = [a_1', ..., a_m', \bar{a}]
\]
\( \alpha' \), being periodic, is a quadratic irrational. However its \( m \) first coefficients \( a_j' (j = 1, ..., m) \) need not be equal to \( a \). They are arbitrary positive integers.

Now consider a lattice of divergence \( \alpha' \) and such that the NN of the origin are all characterized by couples \( (k, r) \) such that \( k \geq m \). Let us write the ratio of the new coordinates \( u_{nk,r}' \)
\[
\phi_{k,r} = -\frac{u_{nk+1,r}'}{u_{nk,r}'} = \frac{(p_{k+1}' + rp_{k+2}') - \alpha'(q_{k+1} + rq_{k+2})}{\alpha'(q_k' + rq_k') - (p_k' + rp_k')}
\]
where \( \frac{p_k'}{q_k} \) is the \( k \)-th principal convergent of \( \alpha' \). In Appendix, we show that, if \( k \geq m \),
\[
\frac{\alpha' q_{k+1}' - p_{k+1}'}{p_k' - \alpha' q_k'} = [\bar{a}] = \alpha = \frac{1}{2} (- a + \sqrt{a^2 + 4}).
\]
It is still easy to generalize what we have done in section 3.6 in order to compute \( \frac{v_{nk,r}'}{v_{nk+1,r}'} \) with the difference, however, that equation (48) no longer holds. We eventually get
\[
\frac{\alpha'}{\frac{v_{nk,r}'}{v_{nk+1,r}'}} \leq \frac{q_k'}{q_{k+1}'} \quad k \text{ even}
\]
\[
\frac{\alpha'}{\frac{v_{nk,r}'}{v_{nk+1,r}'}} \geq \frac{q_k'}{q_{k+1}'} \quad k \text{ odd}
\]
As a consequence, the conclusions reached in the preceding section concerning \( \alpha \) can be extended as well to the larger class of divergences \( \alpha' \), and specially to noble numbers \(^{(1)}\) \( \nu \) of the form

\[
\nu = [a_1, \ldots, a_m, 1, 1, \ldots] = [a_1, \ldots, a_m, 1]
\]

we shall discuss in the next section and more completely in II. However, it is worth noting that for \( k \geq m - 1 \), the recursion relation (10) relative to a noble divergence \( \nu \) is the same as (2), corresponding to a generalized Fibonacci sequence.

As a matter of fact, when a standard parastichy transition \( (q_k + rq_{k+1} \rightarrow q_{k+1} + rq_{k+2}) \) occurs with a divergence \( \nu \) given by (61) for \( k \geq m - 1 \) (and therefore \( r = 0 \)), (10) leads to

\[
q_{k+2} = q_k + q_{k+1}.
\]

This is the same as relation (2). Moreover, the values of the first \( q_k \)'s \( (k < m - 1) \) are arbitrary (they depend on \( \nu \)), so that we automatically get a generalized Fibonacci sequence (Sect. 1.1).

4. Discussion.

As has been shown in the preceding section, the divergence is the main parameter responsible for the shape invariance of a two-dimensional lattice of points. When we compress the lattice along a special direction, the local shape invariance is guaranteed when

A. The development of the continued fraction representing the divergence only allows a sequence of \( a \)'s after some finite stage \( (a \text{ integer } \geq 1) \), and

B. A standard parastichy transition occurs; it is characterized by the fact that each nearest neighbour \( (k, r) \) is replaced by \( (k+1, r) \): \( k \) and \( 0 \leq r < a \) determine the type of principal or intermediate convergent to which the nearest neighbour corresponds.

With respect to property A, all positive integers \( a \) are treated on the same footing. However property B introduces a major distinction among them, strongly favouring \( a = 1 \). Let us consider the two cases \( a = 1 \) and \( a > 1 \) separately.

**Golden or noble divergence: \( a = 1 \).** — When \( a_{k+1} = a_{k+2} = \cdots = 1 \), the standard transition \( (k, r) \rightarrow (k+1, r) \) automatically corresponds to \( r = 0 \) because of condition (38). There is no intermediate convergent as possible nearest neighbour \(^{(12)}\). This means that all NN before and after the transition are principal neighbours and that every parastichy transition is a standard transition, therefore preserving shape invariance (see Fig. 8 where the divergence is the golden divergence \( \tau^{-1} \) which does not allow a single intermediate convergent in its development).

**General « non noble » case: \( a \geq 2 \).** — We have already seen such a case in section 3.6 (divergence \( \alpha = \sqrt{2} - 1 \), corresponding to \( a = 2 \)). Because condition (38) allows \( r = 1 \) when \( a = 2 \), there is always an intermediate neighbour between two consecutive principal neighbours (Fig. 9). As shown above (Tab. I and II) there is at least one non-standard transition (without shape invariance) between two standard transitions. More generally,

\(^{(1)}\) Percival seems to be the first who called noble number an irrational whose development as a continued fraction allows only a sequence of ones after some finite stage [17, 24].

\(^{(12)}\) Coxeter only comments the requirement of the absence of intermediate neighbours as satisfactory from the biological point of view [23].
Fig. 9. — If the divergence \( \alpha \) is irrational but is not a noble number, non-standard transitions occur. On this picture, \( \alpha = \sqrt{2} - 1 = [2] \). a) Parastichies belong to the 2- and 5-families. b) Due to vertical compression of the lattice, a transition has occurred. Parastichies now belong to the 5- and 7-families. Notice how the Voronoi polygon has been distorted. c) Further compressing of the lattice leads to a new transition: 5- and 12-families become visible. The Voronoi polygon recovers the shape it had in (a).

standard and non standard transitions alternate in this case when the plastochrone ratio is continuously reduced. This phenomenon always happens in the presence of intermediate convergents in the development of the divergence as a continued fraction.

Therefore, if we demand shape invariance for each transition, we have to conclude that golden or noble divergence is strongly favoured. Moreover, if we consider spiral phyllotaxis or points aligning along logarithmic spiral, we cannot expect that botanical models can faithfully reproduce them. Look at a daisy or at a sun-flower. The size of florets increases from the center but obviously this increment is not exponential. If the plant « wants » to preserve the shape invariance of the florets, it can do it by reducing the plastochrone ratio radially outwards. This corresponds to a sequence of concentric rings, each one being characterized by a different set of nearest neighbours. Two contiguous rings are separated by a circle of dislocations [16]. These circular defects are much simpler if they correspond to a standard transition and therefore if the nearest neighbours are principal neighbours.

Perhaps the shape invariance requirement is not a definitive argument in favour of golden (noble) phyllotaxis. There is another way to reach the same conclusion which we shall develop in II [20]: to study the close-packing of disks aligning along logarithmic spirals.

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Appendix.

Let us consider some real number \(0 < \gamma < 1\) together with its development as a continued fraction

\[
\gamma = [a_1, a_2, a_3, \ldots, a_k, a_{k+1}, \ldots].
\]  

We assume \(\gamma\) to be irrational so that the sequence of \(a_i\) \((i = 1, 2, \ldots)\) is infinite. The principal convergents of \(\gamma\), say \(\left\{ \frac{p_n}{q_n} \right\}_{n=1,2,\ldots}\), allow a fraction whose numerical value \(y\) is also irrational to be defined

\[
y = \frac{\gamma q_k - p_k}{p_{k-1} - \gamma q_{k-1}}.
\]

If \(\gamma\) is a quadratic irrational, so is \(y\). Solving (A.2) with respect to \(\gamma\) and using (14) and (15), we get

\[
\gamma = \frac{p_k + \gamma p_{k-1}}{q_k + \gamma q_{k-1}} = [a_1, \ldots, a_k, 1/y].
\]

Comparison between (A.1) and (A.3) leads to

\[
y = [a_{k+1}, a_{k+2}, \ldots].
\]

As a consequence, if

\[
\gamma = [a_1, \ldots, a_k, \bar{a}] \quad (a_1, \ldots, a_k \text{ and } a \text{ are arbitrary positive integers})
\]

\(y\) is simply given by

\[
y = [\bar{a}] = \frac{1}{2} \left(-a + \sqrt{a^2 + 4}\right)
\]

and relations (46) and (59) are verified.

If \(a = 1\) in equation (A.5) and (A.6), \(y = \tau^{-1}\) and \(\gamma\) is some noble number (Sect. 1.3 and 3.8). In this case, (A.3) emphasizes the relation between the golden section \(\tau\) and any noble number \(\nu\). As a matter of fact, if

\[
\nu = [a_1, \ldots, a_k, \tau]
\]

has \(\left\{ \frac{p_n}{q_n} \right\}\) as principal convergents, then

\[
\nu = \frac{p_k + \tau^{-1}p_{k-1}}{q_k + \tau^{-1}q_{k-1}}.
\]

Finally, we can still generalize this result. If we replace \(k\) by \(k + 1\) in (A.2), the value of the ratio does not change, so that

\[
\frac{\gamma q_{k+1} - p_{k+1}}{p_k - \gamma q_k} = y = [\bar{a}].
\]
But from (A.2) and (A.9) it follows at once that
\[ \frac{\gamma (q_k + rq_{k+1}) - (p_k + rp_{k+1})}{p_{k-1} + rp_k - \gamma (q_{k-1} + rq_k)} = [\bar{a}] . \] (A.10)

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