Phyllotaxis or the properties of spiral lattices. III. An algebraic model of morphogenesis

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Phyllotaxis or the properties of spiral lattices. III. An algebraic model of morphogenesis (*)

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Résumé. — Une structure phyllotactique comme celles que constituent les écailles d'une pomme de pin prend naissance sur un étroit anneau apical qui entoure un centre local de croissance. On étudie un modèle simple de la morphogenèse d'une telle formation en établissant des relations algébriques *entre permutations des n premiers nombres naturels, chaque nombre correspondant à* l'ordre d'apparition d'une écaille ou d'une feuille. Ce modèle conduit à la définition naturelle d'une divergence. Les valeurs que peut prendre cette divergence s'ordonnent en une structure hiérarchique qui met en évidence le rôle des nombres nobles. Il y a parenté évidente avec l'arbre de Farey que l'on obtient en classant les réseaux de cercles tangents alignés le long de spirales équiangulaires.

Abstract. — A phyllotactical pattern such as the arrangement of the scales of a fir-cone originates along a thin ring surrounding a local center of growth. We study a simple model of the morphogenesis of such a botanical structure by considering algebraic relations between permutations of the n first natural numbers, each number corresponding to the birth order of a given scale or leaf. This model allows to define a divergence angle in a natural way. The possible values of the divergence can be classified according to a hierarchical structure which places the noble numbers in a prominent position. This construction is similar to the Farey-tree obtained in the study of lattices of tangent circles aligned along equiangular spirals.

1. Morphogenesis and phyllotaxis.

1.1 GEOMETERS AND PHYSIOLOGISTS. — Phyllotaxis is the study of spiral or helicoidal patterns one frequently encounters among plants. Its objects are for instance the spiral distribution of florets in a daisy or a sunflower, or the helicoidal arrangement of the scales of a pine cone or a pineapple. The emergence of the Fibonacci sequence in these patterns has been a matter of speculation for a very long time ([1]). Among those people who were interested in this

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([1]) A short account of the history of phyllotaxis may be found in reference [4]. For a general introduction to phyllotaxis, see e.g. references [1] and [5-10].

problem, one notices numerous mathematicians, physicists, crystallographers, naturalists, biologists and even poets such as Goethe who, truly, considered himself as a scientist.

Facing this intrusion of arithmetic into biology, some people see it essentially as a mere consequence of space geometry. They will be called *geometers* in the following. Other scientists look for evidence of the plant metabolism in the geometrical structure of phyllotactic patterns ; they hope to find there how hormones are secreted during the growth of plants. They will be called *physiologists*. They do not deny the role of geometry during morphogenesis. But they emphasize the influence of inhibitors or activators during this process, and want to stress the individual contribution of every chemical substance taking part in the development of the plant.

Recently, a third category of scientists looked at phyllotaxis from a still different point of view. One might call them *physicists* because they consider pure physical systems which exhibit a self-organization very similar to botanical ones [1-3]. Our starting point being far-off, we shall no longer discuss their work in this paper.

From our point of view, the common opposition between those who attribute to genetics a determining role in morphogenesis, and those who think that the essential mechanisms for pattern selection are of an independent nature, needs not to be discussed in the case of phyllotaxis.

It was observed indeed by Snow and Snow [11] in 1935 that by splitting in two parts the apex of *Epilobium hirsutium* (a plant naturally having decussate phyllotaxis), one often obtains two apices developing spiral phyllotaxis. A theoretical approach to this experiment clearly requires a model of the growth which is independent of the genetic information.

1.2 APICAL RING AND MORPHOGENESIS. — Geometers have emphasized the geometrical properties of the phyllotactic pattern : these highly symmetric structures are thought to emerge during growth without call for any particular mechanism ([2]). This point of view was adopted in two papers by Koch and one of us [10] where many references can be found ; as a consequence, the problem of morphogenesis of phyllotactic structures was only a side issue in references [10]. However, in references [12-14] which take up an idea of Marzec and Kappraff [15], the morphogenesis is considered from the point of view of the physiologists : the moulding and growth of the new primordia (as the young shoots are called) on the apical ring is modelled.

As a matter of fact, cellular differentiation producing a new-born shoot does not take place at the tip of the stem or the stalk (apex), but within a ring-shaped region surrounding the apex [7]. This apical ring remains linked to the apex during growth. For an observer on the apex, the new shoots appear to go radially away (Fig. 1).

Let us suppose that the time interval between two successive shoots and the rate of growth have settled down to a stable value. We may then state the problem of phyllotaxis as follows : to explain why the successive shoots appear on the apical ring in a completely ordered way (the angle between two successive shoots becoming approximately constant, after a short transient period) and why, generically, this angular distance is the golden angle (~ 137.5° ...).

This angular distance divided by 2π is called the *divergence*. In « explaining » we aim at giving a deterministic model of the growth on the apical ring, that is, to define a dynamical system which has some reasonable chemical or physical interpretation and does « generically » reproduce the phyllotactic pattern observed.

We assume here that phyllotaxis is the result of a mechanism that can be modelled in the same basic manner in every plant. As was discussed in the introduction, we assume in particular that it is independent of genetics.

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([2]) Or, if such a mechanism does exist, it is hidden and of no special interest to geometers.
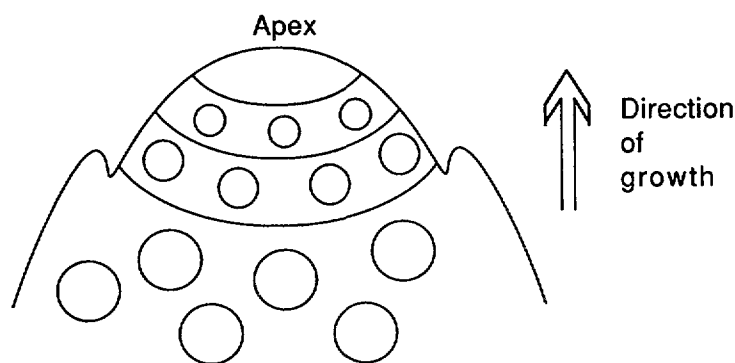
Fig. 1. — The new shoots are born inside a ring-shaped region surrounding the apex of a growing stem. For an observer moving with the apex, the newborn shoots appear to go radially away from the ring where they first appeared.

1.2.1 *A dynamical system on the circle as a chemical model of morphogenesis.* — In order to illustrate the process of apical growth, the authors of references [12-15] advocate the existence of a growth factor interpreted as an inhibitory substance acting as in the case of hydra development [16]. Such a substance will be called « inhibitor » in the following. The inhibitor is one type of « morphogen », a word coined by Turing [17] to specify a chemical substance playing some morphogenetic role during the growth process.

In the case of the hydra, the inhibitor concentration is high in the neighbourhood of a sprouting head ; as long as, and wherever this concentration exceeds some threshold value, no new head is able to develop. As time is elapsing, this morphogen fades away by diffusion or through a chemical reaction [16]. This description has also been used by Thornley to model the growth of a phyllotactic pattern [18].

Consider the inhibitor profile on the apical ring, the result of leaves already placed ; a new leaf will appear at its minimum. Because of this new sprout, the concentration of inhibitor locally increases. Then the whole profile fades away (through diffusion or chemical reaction) until the next leaf appears.

Marzec and Kapraff [15] and Koch, Guerreiro, Bernasconi and Sadik [14] have studied a dynamical system which illustrates this idea ; Douady and Couderc [3] have proposed a physical experiment that exhibits an analogous dynamical behaviour. We shall refer to this general dynamic scheme in the construction of our model.

1.2.2 *The permutation model and the algorithm A.* — We want to describe the growth process by defining a simple deterministic algorithm on the apical ring, following Thornley's scheme [18].

The analytical study of the dynamics of the systems proposed in references [12-15] is extremely difficult ; this is why we shall simplify the model further.

Consider a permutation P_n of the n integers $\{0, 1, . , n - 1\}$ such that $P_n(0) = 0$, and write :

$$P_n = \begin{pmatrix} 0 & 1 & . & n-1 \\ 0 & C_1 & . & C_{n-1} \end{pmatrix} . \tag{1}$$

We can think of P_n as defining the state of our « discrete time dynamical system » at time n : imagine a distribution of n points on a circle and associate an integer C_j to each point so that, when the circle is given an orientation, one successively meets the integers 0, C_1, C_2, . , C_{n-1} around the circle (see Fig. 2).
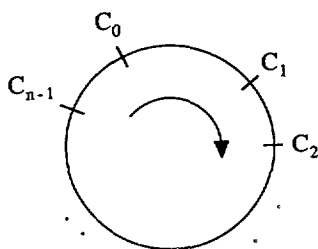
Fig. 2. — The distribution of integers $C_0 = 0$, C_1, C_2, .. , C_{n-1} around the circle.

Now this geometrical picture of P_n is a simple representation of the state of the apical ring at time n : the point labelled by $i - 1$ indicates where the i-th sprout is born ; moreover, birth of the n-th sprout has just occurred at time n. *Permutation P_n thus provides us with one state for the system.* Let us now give an evolution law, reproducing the growth process sketched in 1.2.1.

Consider the system at time $n = 2$; its state is given by the trivial permutation P_2 (Fig. 3). At the next step, the symmetry is broken ; we have to decide arbitrarily on which side of point 0 we place point 2 (Fig. 4).
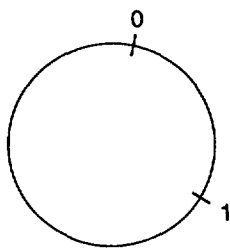

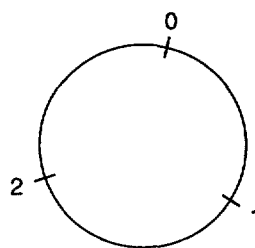Fig. 3.   Fig. 4.

Fig. 3. — If one disregards the value of the angles, there is only one possible ordering of two points along the circle.

Fig. 4. — The symmetry is broken as soon as a third point (here point number 2) is located on the circle.

All the following points will be placed according to an algorithm that takes the principle stated in 1.2.1 into account as simply as possible : *at each step, we are looking for the absolute minimum of the inhibitor concentration*, that is, we try to place point n as far as possible from the latest ones.

Point 3 is therefore placed between 0 and 1 (Fig. 5). Suppose now that 3 has been placed « very close » to 0 (because 0 is the oldest point). We should then place 4 between the oldest point after 0 (namely 1) and its older neighbour (namely 2). We argue again that 4 is placed « very close » to 1, so that 5 has to be put between 2 and its older neighbour, namely 0 (Fig. 6).

0 has thus been given a new neighbour (5), replacing 2, so that the rule can be repeated for the following points.

Let us sum up our algorithm : denote by $A_i^{(n)}$ the older neighbour of i in P_n. Suppose that n has been placed next to 0 in P_n at time n. Then at time $n + 1$, set $n + 1$ between 1 and $A_1^{(n+1)}$; at time $n + k$, put $n + k$ between k and $A_k^{(n+k)}$
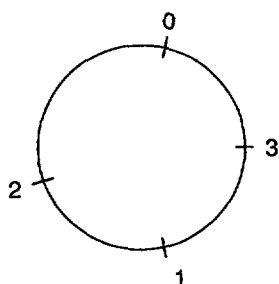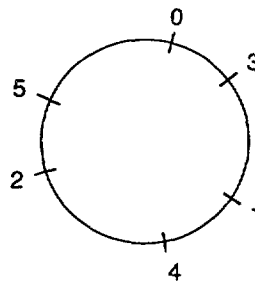
Fig. 5.

Fig. 6.

Fig. 5. — Algorithm A demands point 3 to be located between points 0 and 1.

Fig. 6. — Distribution of six points according to algorithm A.

Now there exists j such that $A_j^{(n+j)} = 0$, $A_k^{(n+k)} \neq 0$ $\forall k < j$; set then $n + j$ between j and $A_j^{(n+j)} = 0$, and begin again : Put $n + j + 1$ between 1 and $A_j^{(n+j+1)}$, and so on.

Applying this algorithm to permutation $P_3 = \begin{pmatrix} 0 & 1 & 2 \\ 0 & 1 & 2 \end{pmatrix}$, we obtain at time 15

$$P_{15} = \begin{pmatrix} 0 & 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 & 11 & 12 & 13 & 14 \\ 0 & 8 & 3 & 11 & 6 & 14 & 1 & 9 & 4 & 12 & 7 & 2 & 10 & 5 & 13 \end{pmatrix} .$$

Let us call A the algorithm we have just constructed. We don't claim that the evolution law defined by A perfectly mimics the dynamical behaviour of a real system following Thornley's scheme. Our algorithm never forgets the older sprouts nor does it take into account the exact location of their birth on the apical ring. Nevertheless, it gives a good insight into what may happen at the beginning of the growth. Stationary regimes of growth should also be described by permutations ; we shall return later to this point.

Anyway algorithm A exhibits the two main features we would expect from a dynamical system on the circle modelling phyllotaxis :

— the shoots organize themselves so as to produce a constant angular distance between any shoot and the immediately older one ;

— this angular distance divided by 2π is the golden divergence.

The aim of this paper is to express these assertions mathematically and to prove them. A general description of the construction and properties of permutations displaying the first feature will also be given. Algorithm A can also produce bijugate or trijugate phyllotactic patterns. We will discuss this last property without giving any mathematical proof, for the sake of brevity.

2. Angular permutations.

2.1 DEFINITIONS.

2.1.1 *The set of divergences.* — The main parameter that characterizes an idealized phyllotactic pattern is its divergence, that is, a number in $[0, 1[$ (recall that the divergence is an angular distance divided by 2π).

We will consider divergences belonging to $\left[0, \frac{1}{2} \right]$ throughout the whole paper, without loss of generality : they are related to divergences in $\left[\frac{1}{2}, 1 \right]$ by a mere inversion of the orientation of the circle.

A dynamical system modelling phyllotaxis should generically select a unique value within the set of possible divergences ; this number is the *Fibonacci* or *golden divergence*, that is :

$$\theta_F = 0.381966 = \tau^{-2}$$

It is defined with the help of the golden mean :

$$\tau = \frac{\sqrt{5} + 1}{2}$$

which has the well known property of being the « worst » irrational ; in other words, it is the irrational the « most slowly » approximated by sequences of rational fractions [19, 20].

Any real number α between 0 and 1 can be represented in a unique way as a continued fraction

$$\alpha = \cfrac{1}{a_1 + \cfrac{1}{a_2 + \cfrac{1}{a_3 + \cdot}}} = [a_1, a_2, a_3, . \ ] \tag{2}$$

where each a_i is a positive integer. The representation (2) is unique, except if α is a rational. In the latter case, the continued fraction is finite and the ambiguity is removed if one requires that the last term of the development (2) exceeds 1. As a consequence, every α belonging to $\left] 0, \frac{1}{2} \right]$ has a development of the form

$$\begin{cases} \alpha = [a_1 ; . \ ] & \alpha \ \text{irrational} \\ \alpha = [a_2 ; . \quad ; a_n] & \alpha \ \text{rational} \end{cases} \ a_1, a_2, a_n \ \text{integers} > 1 \tag{3}$$

θ_F has a particularly simple development :

$$\theta_F = [2, 1, 1, 1, . \ ] = [2, \bar{1}] \tag{4}$$

where a periodic sequence is represented by its period overlined. On the other hand, the *Lucas divergence* [3] θ_L, which is the main anomalous divergence observed in nature, is given by :

$$\theta_L = \frac{1}{3 + \tau^{-1}} = [3, \bar{1}] . \tag{5}$$

Those irrational numbers, whose development consists of an infinite sequence of ones after some stage, are called *noble numbers* [4]. One notices that θ_F and θ_L are the « simplest » noble numbers in $\left[0, \frac{1}{2} \right]$.

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[3] Biologists prefer to use divergence angles expressed in degrees and belonging to the interval $]0°, 180°]$. According to this rule, they speak of the golden angle, or Fibonacci angle, equal to $360° . (1 - \tau^{-1}) = 137°, 507 ...$ In the same spirit, they replace the Lucas divergence by the Lucas angle equal to $360° . (3 + \tau^{-1})^{-1} = 99°, 501 ..$

[4] Any noble number ν can be written as $\nu = \frac{a\tau + b}{c\tau + d}$ where a, b, c and d are integers such that $|ad - bc| = 1$.

2.1.2 *Definition.* — Each P_n (relation (1)) can be written as

$$P_n = \begin{pmatrix} 0 & 1 & . & n-1 \\ C_0 & C_1 & & C_{n-1} \end{pmatrix} . \tag{6}$$

P_n is a permutation of $N_{n-1} = \{0, 1, . , n-1\}$ subjected to

$$C_0 = 0 . \tag{7}$$

For convenience, define C_n through

$$C_n = C_0 = 0 . \tag{8}$$

As discussed above, P_n represents a sequence of integers $C_0, C_1, .. , C_{n-1}$ on a circle, according to a predefined orientation (Fig. 7). If we disregard the exact location of each integer on the circle, we have a one-to-one correspondence between the set of permutations and these geometrical pictures.

We shall call P_n an *angular permutation* if there exists $\theta \in]0, 1[$ such that

$$0 = \{C_0 \theta\} < \{C_1 \theta\} < \cdot \quad < \{C_{n-1} \theta\} < 1 \tag{9}$$

(where $\{x\}$ denotes the fractional part of the number x). We shall say that θ is a *divergence compatible* with P_n and write div (P_n) the set of divergences compatible with P_n. It is easy to check that $\theta = 0.35$ is compatible with the permutation shown in figure 7.

We can construct a geometrical picture of an angular permutation P_n by placing the points C_i on the circle at an angular distance $2\pi . \{C_i \theta\}$ from C_0, where $\theta \in$ div (P_n). In this case, we have a *realization* $T_n(\theta)$ of P_n (Fig. 8).
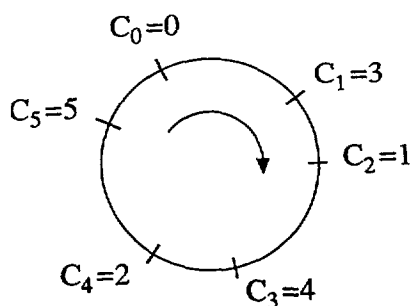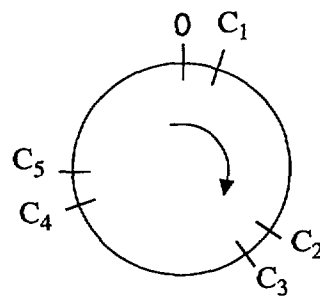

Fig. 7.   Fig. 8.

Fig. 7. — Circular representation of permutation

$$P_6 = \begin{pmatrix} 0 & 1 & 2 & 3 & 4 & 5 \\ C_0 & C_1 & C_2 & C_3 & C_4 & C_5 \end{pmatrix} .$$

The number $\theta = 0.35$ is a divergence compatible with P_6 because $0 = \{0.35\,C_0\} < \{0.35\,C_1\} < \{0.35\,C_2\} < \{0.35\,C_3\} < \{0.35\,C_4\} < \{0.35\,C_5\}$. (See relation (9)). As a consequence, P_6 is angular.

Fig. 8. — Realization $T_6(0.35)$ of the angular permutation P_6 of figure 7. The angular distance between 0 and C_i equals $2\pi. \{C_i \theta\}$. The relative order of the points C_i is the same as in figure 7.

Notice that it is equivalent to represent a permutation on a circle or on the segment [0, 1 [. In particular, the extension of the definition of $T_n(\theta)$ to the latter case is immediate. The circle merely allows a closer connection to phyllotaxis.

2.2 THE CUT-AND-PROJECTION METHOD. — The study of angular permutations is equivalent to the following problem: given a number $\theta \in {]}0, 1{[}$, how are the numbers $\{\theta\}$, $\{2\,\theta\}, . , \{n\theta\}$ ordered on the segment $[0, 1]$?

The geometrical analysis of quasicrystals has been simplified by the well-known cut-and-projection method [21-25]. Similarly, the problem of ordering $\{\theta\}$, $\{2\,\theta\}$, ..., $\{n\,\theta\}$ on the circle or on the segment $[0, 1[$ is greatly simplified by a lift in two dimensions and by the introduction (in the following section) of a two-dimensional periodic lattice ($W_{nm}(\theta)$-lattice) and by the choice of a subset of this lattice, the strip $\overline{b}_L$, to be defined in section 2.2.4.

2.2.1 *The $W_{nm}(\theta)$-lattice.* — We define the $W_{nm}(\theta)$-lattice by

$$W_{nm}(\theta) = \left\{ n \begin{pmatrix} \theta \\ 1 \end{pmatrix} + m \begin{pmatrix} 1 \\ 0 \end{pmatrix} ; n, m \text{ integers} \right\} \tag{10}$$

where $\theta \in {]}0, 1{[}$ is called the *divergence of the lattice.* In order to simplify, we assume θ to be irrational; as a consequence two distinct points of the lattice never have the same x-coordinate [5]. A point of the lattice will be written

$$W_{nm} = n \begin{pmatrix} \theta \\ 1 \end{pmatrix} - m \begin{pmatrix} 1 \\ 0 \end{pmatrix} \tag{11}$$

(notice the minus sign chosen for convenience). For any pair of integers (k, l) we have

$$k W_{nm} + l W_{n'm'} = W_{kn + ln', km + lm'} . \tag{12}$$

The interest of this construction is that, if W_{nm} is such that $0 \leqslant W_{nm}^x < 1$ and $W_{nm}^y > 0$, then,

$$W_{nm} = \begin{pmatrix} \{n\theta\} \\ n \end{pmatrix} . \tag{13}$$

Such a point can be unambiguously written $W_{nm} = W_n$.

2.2.2 *Convex envelopes of the $W_{nm}(\theta)$-lattice.* — Relation (13) directly connects the $W_{nm}(\theta)$-lattice with the realization $T_k(\theta)$ of an angular permutation P_k. For future convenience, we recall the construction of convex envelopes which simplifies the study of the structure of $T_k(\theta)$ [26].

In any periodic plane lattice one can construct two broken lines P_- and P_+ which are the convex envelopes of the lattice restricted to the two parts of the upper half-plane defined by $(x < 0, y > 0)$ and $(x > 0, y > 0)$ (Fig. 9). Envelopes P_- and P_+ describe the neighbourhood of point 0 (the origin) and, therefore, because of the periodicity of the lattice, of any lattice point. In order to state a well known but very important proposition on convex envelopes of the $W_{nm}(\theta)$-lattice, we recall in the next section the main properties of the convergent of an irrational number $\theta = [a_1, a_2, . , a_k, .] \in {]}0, 1{[}$.

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[5] We shall call the two components $\begin{pmatrix} a \\ b \end{pmatrix}$ of a vector x-coordinate and y-coordinate rather than abscissa and ordinate.
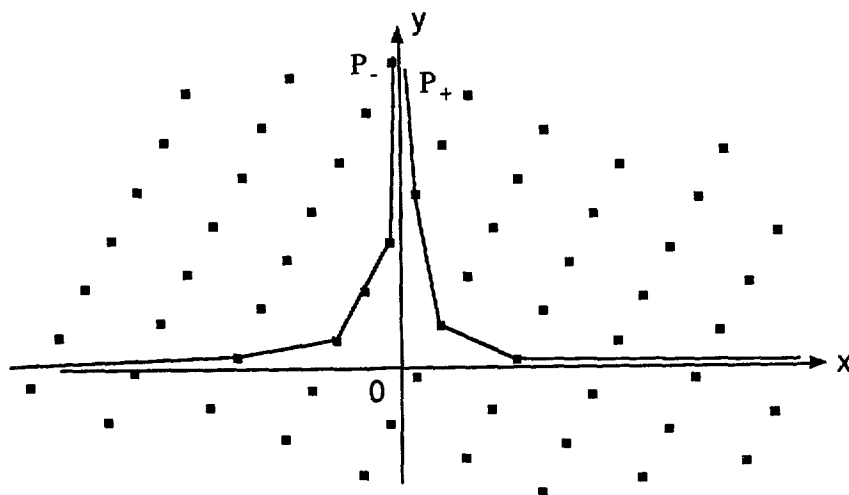
Fig. 9. — The two convex envelopes P_+ and P_- on the upper plane of a point lattice $W_{nm}(\theta)$.

2.2.3 *Convergents of a continued fraction.* — From the continued fraction representation of an irrational $\theta = [a_1, a_2, . \ , a_k, . \ ]$, one defines an infinite sequence of rational fractions

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

$$\frac{p_3}{q_3} = [a_1, a_2, a_3]$$

$$..$$

$$\frac{p_n}{q_n} = [a_1, a_2, . \ , a_n] \qquad\qquad\qquad\qquad (14)$$

defined by truncating the development of θ after the n-th term. The fractions $\dfrac{p_n}{q_n}$ are known as the *principal convergents* of the irrational number θ. They satisfy the relations

$$\begin{aligned} p_{n+2} &= a_{n+2} \, p_{n+1} + p_n \\ q_{n+2} &= a_{n+2} \, q_{n+1} + q_n \end{aligned} \qquad (n \geqslant 0) \qquad\qquad (15)$$

with

$$\begin{aligned} p_0 &= 0 \qquad p_1 = 1 \\ q_0 &= 1 \qquad q_1 = a_1 \ . \end{aligned} \qquad\qquad\qquad (16)$$

Further properties can be found in references [19, 20]. In particular

$$\frac{p_{2n}}{q_{2n}} < \theta < \frac{p_{2n+1}}{q_{2n+1}} \qquad \left| \theta - \frac{p_r}{q_r} \right| > \left| \theta - \frac{p_s}{q_s} \right| \qquad (s > r) \qquad (17)$$

$(n, r, s \geqslant 0)$.

The *intermediate convergents* of θ are defined in the following way. If $a_{k+2} > 1$ for some $k \geq 0$, one constructs the rational fractions

$$\frac{p_k}{q_k}, \quad \frac{p_k + p_{k+1}}{q_k + q_{k+1}}, \quad \frac{p_k + 2\,p_{k+1}}{q_k + 2\,q_{k+1}}, \ldots, \frac{p_k + a_{k+2}\,p_{k+1}}{q_n + a_{k+2}\,q_{k+1}} = \frac{p_{k+2}}{q_{k+2}} \tag{18}$$

Because of (17), $\dfrac{p_k}{q_k}$ and $\dfrac{p_{k+2}}{q_{k+2}}$ are both either smaller or larger than θ according to the parity of k. The fractions $\dfrac{p_{k,r}}{q_{k,r}} = \dfrac{p_k + rp_{k+1}}{q_k + rq_{k+1}}$, for $0 < r < a_{k+2}$, are called *intermediate convergents* of θ. Together with the principal convergents, they are, in a way which has to be specified, the best rational approximations of the irrational θ [19, 20]. This last property has a geometrical counterpart, which can be expressed through

Proposition 1 :

In a $W_{nm}(\theta)$-*lattice, the envelope* $P_-(P_+)$ *goes through points* $Wq_{n,r}p_{n,r}$. *Here* $0 \leq r \leq a_{n+2}$ *and n is odd (even).*

Proposition 1 is demonstrated in Appendix A. Notice that, because of (18), the segment of the envelope joining $Wq_k p_k$ with $Wq_{k+2} p_{k+2}$ is a straight line, with points $Wq_{k,r}p_{k,r}$ $(0 < r < a_{k+2})$ dividing this segment into equal parts. As a consequence, the vertices of the envelope correspond to principal convergents $Wq_k p_k$.

2.2.4 Lattice strips and neighbouring points. — We now need a lattice subset of $W_{nm}(\theta)$ whose projection onto the x-axis yields the set of points $\{C,\ \theta\}$ on the segment $[0, 1[$ of the horizontal axis. This is best done through the following definition (Fig. 10).
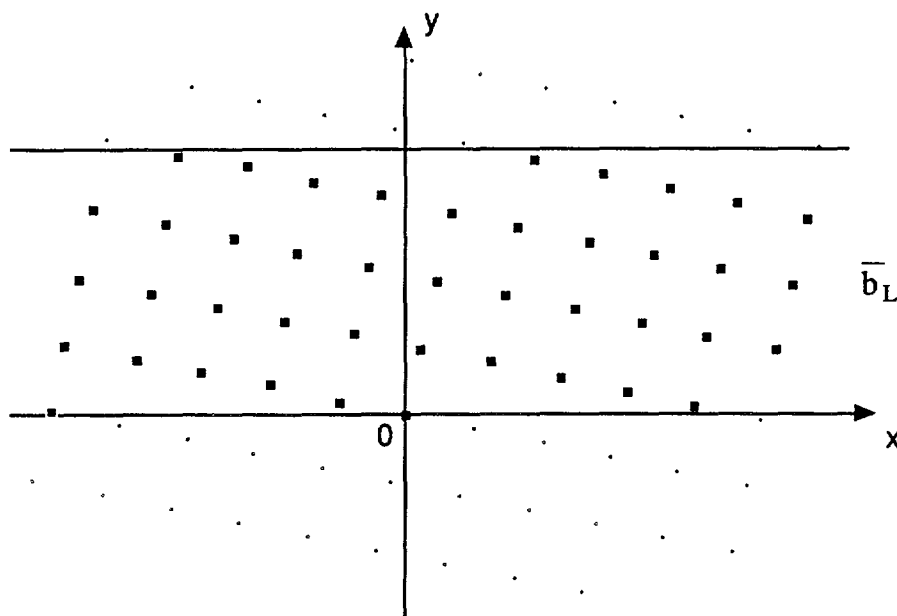

Fig. 10. — The extended lattice strip $\bar{b}_L$ defines a subset of the point lattice $W_{nm}(\theta)$. The projection of the points of $\bar{b}_L$ onto the x-axis allows to order the fractional parts $\{n\theta\}$ on the segment $]0, 1[$ $(0 < n \leq L)$.

We call *extended lattice strip* $\overline{b}_L$ the set

$$\overline{b}_L = W_{nm}(\theta) \cap R \times [0, L] = \{W_{nm} ; n \in N_L, m \in Z\} \tag{19}$$

where $L \in N$.

In the same way, we call *lattice strip* b_L the set

$$b_L = W_{nm}(\theta) \cap [0, 1[\times [0, L] = \{W_0, W_1, . , W_L\} . \tag{20}$$

Because of (13), the projection of b_L onto the x-axis directly yields the realization $T_{L+1}(\theta)$ of the corresponding angular permutation P_{L+1}.

Clearly, the knowledge of the neighbourhood of each $W_i \in b_L$ allows one to build $T_{L+1}(\theta)$. Because of the periodicity of the lattice $W_{nm}(\theta)$, the structure of P_- and P_+ determines this neighbourhood. The corresponding analysis, although simple in principle, is somewhat cumbersome. However, it leads to an important proposition stated in the next section (Prop. 2) which allows an angular permutation to be characterized.

2.3 CHARACTERIZATION OF ANGULAR PERMUTATIONS. — Given any permutation $P_n = \begin{pmatrix} 0 & 1 & n-1 \\ C_0 & C_1 . & C_{n-1} \end{pmatrix}$, is it angular ? The following proposition brings together a result of Swierczkowski who followed a conjecture by Steinhaus [27], and its reciprocal.

Proposition 2 :

A permutation P_n is angular if and only if the differences

$$C_{i+1} - C_i \qquad (i = 0, 1, . , n-1)$$

take only two values

$$\alpha \quad and \quad -\beta \quad (\alpha, \beta \text{ positive integers})$$

and possibly a third value

$$\gamma = \alpha - \beta$$

which can only occur if i is different from 0 or $n-1$.

All the material necessary for the demonstration of proposition 2 can be found in Appendix B. Figures 11a and 11b show two angular permutations P_7 and P_8. In the latter case, there occur only two differences, namely $\alpha = 3$ and $-\beta = -5$ while $\gamma = -2$ also appears in the former case. Figure 11c, on the other hand, shows a permutation P_8 which is not angular.

Moreover, proposition 2 has an obvious consequence. If P_n is an angular permutation, the new permutation P'_n obtained by replacing C_i by C_{q-i} for all i between 1 and $q-1$ is still angular. This means that the choice of the orientation on the circle has no influence on the angularity of the corresponding permutation.

2.3.1 *How to classify angular permutations ?* — Our purpose is to apply the concept of angular permutation to phyllotaxis. As we shall see below, it will be necessary to emphasize the geometrical aspect of this concept. Moreover, we shall need to classify the various angular permutations as an access road toward the morphogenesis of a phyllotactic structure. To this aim, we state a new proposition which will be useful for such a classification.
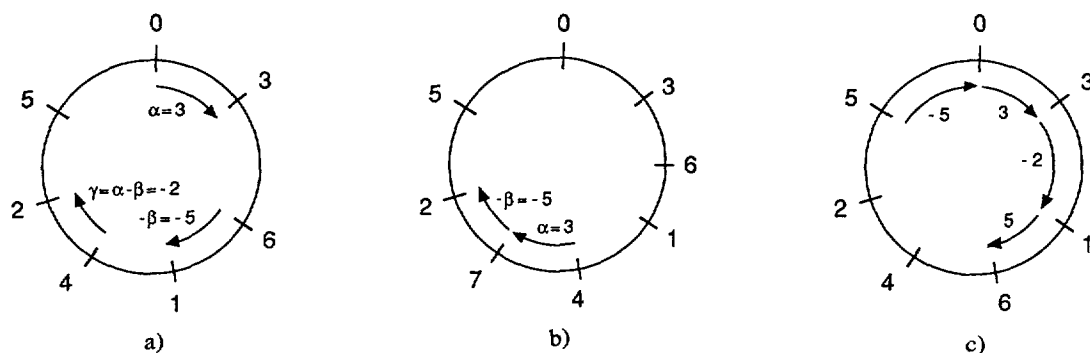
Fig. 11. — The permutation $P_7(\tau^{-2})$ shows three differences $C_{i+1} - C_i$ which satisfy the requirements of Proposition 2 (Fig. 11a). In the case of $P_8(\tau^{-2})$ shown in figure 11b, the third difference $\gamma = -2$ is missing. Permutation P_7 shown in figure 11c is not angular (there are four differences).

Proposition 3 :

For any triple (α, β, n) of positive integers which satisfies the two conditions [6] :

$$(\alpha, \beta) = 1$$
$$\max [\alpha, \beta] + 1 \leq n \leq \alpha + \beta \tag{21}$$

there exists a unique angular permutation P_n such that $C_1 = \alpha$, $C_{n-1} = \beta$.

Proposition 3 is demonstrated in Appendix B. Moreover, as a consequence of propositions 2 and 3, there exists a one-to-one correspondence between the set of triples described in proposition 3 and the set of angular permutations. The connection is given by the relation

$$\alpha = C_1 \qquad \beta = C_{n-1} . \tag{22}$$

Actually, in any angular permutation P_n, the triple (C_1, C_{n-1}, n) satisfies the conditions (21). Notice that *the permutations characterized by a triple $(\alpha, \beta, \alpha + \beta)$ are those for which the differences $C_{i+1} - C_i$ $(i = 0, 1, . , n - 1)$ take only the two values*

$$\alpha \quad and \quad -\beta \qquad (\alpha, \beta \text{ positive integers}) .$$

This property is a direct consequence of lemma B.2 (Appendix B).

3. Hierarchy of angular permutations.

Proposition 3 allows one to set up a classification among angular permutations. The hierarchy which emerges will in turn be very useful in order to make a connection with the morphogenesis of a phyllotactic structure. To make this connection manifest, we shall underline the geometrical interpretation of a permutation P_n as a series of integers $C_0, C_1, . , C_{n-1}$ placed on a circle.

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[6] (α, β) denotes the highest common divisor of two positive integers α and β. Conditions (21) therefore expresses the fact that α and β are coprime.

3.1 DESCENT AND ANGULAR DESCENT. — Let us consider some permutation P_n. We shall note $P_n^{(n-1)}$ the permutation obtained from P_n by removing point number $n-1$:

$$P_n = \begin{pmatrix} 0 & 1 & k-1 & k & k+1 & . & n-1 \\ 0 & C_1 & . & C_{k-1} & C_k = n-1 & C_{k+1} & . & C_{n-1} \end{pmatrix} \Rightarrow$$

$$P_n^{(n-1)} = \begin{pmatrix} 0 & 1 & k-1 & k & k+1 & . & n-2 \\ 0 & C_1 & . & C_{k-1} & C_{k+1} & C_{k+2} & . & C_{n-1} \end{pmatrix} . \quad (23)$$

We choose the same orientation for P_n and $P_n^{(n-1)}$ on the circle. We can now introduce two definitions.

We shall call *descent* $D(P_n)$ *of a permutation* P_n the set of the permutations P_{n+1} for which ([7])

$$P_{n+1}^{(n)} = P_n . \quad (24)$$

In particular, the subset of $D(P_n)$ consisting of all angular permutations $\in D(P_n)$ will be called the *angular descent* of P_n.

Notice that the word « descent » is used here in the sense of « lineage ». The reason of this choice will appear below to be justified by the connection between the concept of angular descent and the emergence of a phyllotactic pattern.

3.1.1 *Angular descent of an angular permutation.* — Let $P_n = (\alpha, \beta, n)$ be an angular permutation.

A natural question arises now : does it have an angular descent ? In other words, where can we put a further point (with number n) in P_n so that the resulting permutation P_{n+1} is still angular ?

Before answering this question, we notice a simple property of angular permutations. If some permutation P_n is angular, then P_{n-1}, defined through

$$P_n \in D(P_{n-1}) \quad (25)$$

is angular : this is an obvious consequence of the definition (9).

We have therefore

Proposition 4 :

If an angular permutation P_n belongs to the descent of a permutation P_{n-1}, then P_{n-1} itself is angular.

Conversely, to show that P_{n+1} can be angular when P_n is, we have to consider two cases.

1. *The new point n is a neighbour of the origin* 0.

For definiteness, let us set n between β *and* 0 (Fig. 12).

The permutation P_{n+1} thus defined is clearly angular if $n = \alpha + \beta$. For, in this case, P_n was characterized by only two differences $C_{i+1} - C_i$, namely α and $-\beta$ (see Sect. 2.3.1). As a consequence, P_{n+1} itself displays the three differences $-n$, α and $-\beta = \alpha - n$ which satisfy conditions of proposition 2. On the other hand, if $n < \alpha + \beta$, it is easy to check that P_{n+1} shows more than three differences.

The same conclusion holds for n between 0 and α because of the symmetry of the roles that α and β play in the characterization of a permutation.

([7]) In other words, the descent of a permutation P_n is the set of all permutations obtained from P_n by adjunction of a supplementary point, namely point n.
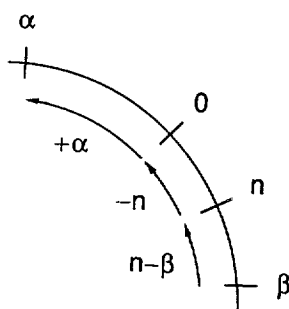
Fig. 12. — The new point n has been put between 0 and β, a former neighbour of the origin. The new corresponding permutation P_{n+1} is characterized by three differences $n - \beta = \alpha$; $-n$; $-\beta$ if $n = \alpha + \beta$. If $n < \alpha + \beta$, the number of differences exceeds three.

To summarize, *the resulting permutation P_{n+1} is angular if and only if*

$$n = \alpha + \beta . \tag{26}$$

2. *The new point n is not a neighbour of the origin 0.*

One can use proposition 3 which claims that there is a unique way to construct an angular permutation P_{n+1} defined by the triple $(\alpha, \beta, n+1)$ provided that $n + 1 \leqslant \alpha + \beta$ (when $n + 1 > \alpha + \beta$, this is impossible). Because of proposition 4, $P_{n+1} \in D(P_n)$, as required. On the other hand, P_n itself is angular, which implies $n \leqslant \alpha + \beta$. In order to reconcile the latter inequalities, one must clearly require

$$n < \alpha + \beta . \tag{27}$$

We can summarize this discussion in table I.

Table I.

1. $n = \alpha + \beta$		
	$(\alpha, n, n+1)$	
(α, β, n)		*Bifurcation*
	$(n, \beta, n+1)$	
2. $n < \alpha + \beta$		
$(\alpha, \beta, n) \longrightarrow (\alpha, \beta, n+1)$		

3.1.2 *Descent tree of angular permutations.* — Apart from the detail of the transition $(\alpha, \beta, n) \to (\alpha, \beta, n+1)$, table I defines the *algorithm of angular descent* which allows us to state the lineage between some angular permutation P_n . (α, β, n) and any member of its descent. Since any angular permutation P_n is the descent of an angular permutation $P_n^{(n-1)}$ (Prop. 4), it is clear that we can obtain all the angular permutations by application of the algorithm of angular descent to $(1, 2, 3)$ and $(2, 1, 3)$. The whole set of angular permutations therefore constitutes two trees ; one can be obtained from the other by inverting the orientation of the circle or, equivalently, by substituting to a compatible divergence θ the new one $1 - \theta$.

According to the convention made in section 2.1.1, *we restrict ourselves* to divergences belonging to $\left[0, \frac{1}{2}\right]$ and, therefore, *to the tree constituted by* $(1, 2, 3)$ *together with its whole angular descent* [8].

3.1.3 *Algorithm of angular descent.* — We have described above the general structure of the algorithm of angular descent, but it is interesting to see explicitly how the transition

$$(\alpha, \beta, n) \to (\alpha, \beta, n + 1) \tag{28}$$

takes place (recall that (28) is subjected to condition 27)).

Consider figure 13. Let point $n - 1$ be located between points A_{n-1} and B_{n-1} (A_{n-1}, $n - 1$ and B_{n-1} are successive points in P_n). Let A_n and B_n be two points such that point n will be located between them in P_{n+1}, the angular descent of P_n; according to the orientation, one successively meets A_n, n and B_n. There are two possibilities.

1. $\alpha < \beta$, so that $\alpha - \beta < 0$. As a consequence, the only positive difference is α. Therefore, $\delta_1 = \alpha$, $\delta_1' = \alpha$ and $A_n = A_{n-1} + 1$: n must be located directly after $A_n = n - \alpha$ for P_{n+1} to be angular.

2. $\alpha > \beta$. One can show similarly that n has to be located directly before $B_n = n - \beta$ for P_{n+1} to be angular.
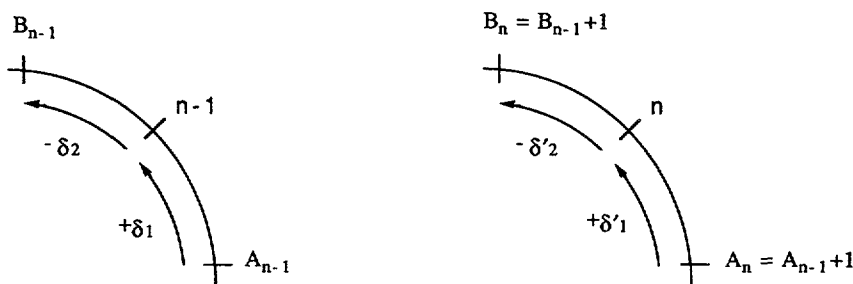
Fig. 13. — Algorithm of angular descent : Points number $n - 1$ and n correspond to symmetrical situations (see text).

3.2 THE SET OF COMPATIBLE DIVERGENCES. — We have already introduced the set div (P_n) = div (α, β, n) of the divergences θ that are compatible with the permutation $P_n = (\alpha, \beta, n)$. Our aim is to determine this set.

To answer this question we have first to state

Proposition 5 :

If $n \geqslant 3$ points are located on a circle, and the position of point number k is given by the angle $\{k\theta\}$, where θ is irrational and the integer k satisfies $0 \leqslant k \leqslant n - 1$, then k_1 and k_2, the two neighbours of the origin (i.e. point number 0), satisfy

$$k_1 = q_{m, r} \qquad k_2 = q_{m+1} \tag{29}$$

for some m and $r (1 \leqslant r \leqslant a_{m+2})$.

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(8) Here, this includes the « whole lineage » of P_n and not only its direct offsprings.

Integers $q_{m,r}$ and q_{m+1} are denominators of two convergents $\dfrac{p_{m,r}}{q_{m,r}}$ and $\dfrac{p_{m+1}}{q_{m+1}}$ of θ. Moreover, any integer equal to some other denominator $q_{s,t}$ of a convergent of θ such that

$$q_{s,t} > \max\ [q_{m,r}\ ;\ q_{m+1}] = q_{m,r} \tag{30}$$

is larger than n.

Proposition 5 is a direct consequence of Lemma B.1 (Appendix B). Moreover, it shows that div (α, β, n) is the set of those θ for which

$$q_{m,r} = \alpha \qquad q_{m+1} = \beta \qquad \text{if} \qquad \alpha > \beta \tag{31}$$

or

$$q_{m,r} = \beta \qquad q_{m+1} = \alpha \qquad \text{if} \qquad \alpha < \beta\ . \tag{32}$$

Notice that θ needs not to be irrational for proposition 5 to be true. If the numbers $\{k\theta\}$ are all distinct for $0 \leqslant k \leqslant n - 1$, proposition 5 also applies, even if θ is rational.

3.2.1 *Computing the set of compatible divergences.* — We have to compute the set div (α, β, n) with the condition

$$\text{div}\ (\alpha, \beta, n) \subset \left[0, \frac{1}{2}\right] \tag{33}$$

(see 2.1.1). Now proposition 5 shows that determining div (α, β, n) is equivalent to the construction of the continued fraction from two integers α and β which are known to satisfy (31) or (32) for some (*a priori* unknown) m and r.

Such a construction is well known (see Ref. [10]). We sketch it here briefly.

Let us start with the relation

$$q_{m,r} = rq_{m+1} + q_m \qquad 1 \leqslant r \leqslant a_{m+2} \tag{34}$$

which is a generalization of (15) for intermediate convergents (see (18)). (34) implies

$$0 \leqslant q_m = q_{m,r} - rq_{m+1} < q_{m+1} \tag{35}$$

or

$$a_{m+2} \geqslant r = \left[\frac{q_{m,r}}{q_{m+1}}\right] \tag{36}$$

where $[s] = s - \{s\}$. From (34) r is the Euclidean divisor $\dfrac{q_{m,r}}{q_{m+1}}$ with remainder q_m. Similarly,

$$a_{m+1} = \left[\frac{q_{m+1}}{q_m}\right] \tag{37}$$

is the divisor $\dfrac{q_{m+1}}{q_m}$ with remainder q_{m-1}, and so on. Now, for any couple of principal convergents,

$$(q_{m+1}, q_m) = 1 \qquad \text{if} \quad m \geqslant 0 \tag{38}$$

so that the remainder of the division $\dfrac{q_{m+1}}{q_m}$ vanishes if and only if $q_m = 1$. (33) implies that

$$q_0 = 1 \qquad q_1 = a_1 > 1 \tag{39}$$

so that $m = 0$ when the Euclidean algorithm of division stops.

We can now summarize our results as follows.

An angular permutation (α, β, n) determines in a unique way the first part of the development of θ as a continued fraction, namely $a_1, a_2, . , a_{m+1}$. Moreover, it sets $r \leq a_{m+2}$ and leaves the rest of the elements $a_{m+3}, a_{m+4}, .$ undetermined. In other words, if

$$\theta = [a_1, a_2, . , a_{m+2}, .] = [a_1, a_2, . , a_{m+1}, r_{m+2}] \tag{40}$$

with

$$r_{m+2} = [a_{m+2}, a_{m+3}, .] = a_{m+2} + \dfrac{1}{r_{m+3}} \tag{41}$$

one has the simple condition

$$r \leq r_{m+2} . \tag{42}$$

We shall symbolize the set of continued fractions which satisfy this property by

$$\operatorname{div}(\alpha, \beta, n) = [a_1, . , a_{m+1}, r+] . \tag{43}$$

As noted above, the result obtained here can be extended to rational divergences, provided that we restrict (42) through

$$r < r_{m+2} < \infty \tag{44}$$

which insures that, if $\theta = \dfrac{p}{q}$ is rational, then $q > n$ so that all points of the realization of the permutation (α, β, n) are distinct.

We can sum up the results of this lengthy discussion through

Proposition 6 :

Let (α, β, n) be a permutation such that $\operatorname{div}(\alpha, \beta, n) \subset \left[0, \dfrac{1}{2}\right]$. *Then α and β determine a series of integers $a_1, a_2, . , a_{m+1}, r$ for which the following relation hold*

$$\operatorname{div}(\alpha, \beta, n) =]\theta_1, \theta_2[\tag{45}$$

and, if m is even,

$$\theta_2 = [a_1, a_2, . , a_{m+1}] > [a_1, a_2, . , a_{m+1}, r] = \theta_1 \tag{46}$$

while, if m is odd,

$$\theta_1 = [a_1, a_2, . , a_{m+1}] < [a_1, a_2, . , a_{m+1}, r] = \theta_2 \tag{47}$$

so that we write

$$\operatorname{div}(\alpha, \beta, n) = [a_1, . , a_{m+1}, r+] . \tag{48}$$

For example, compute div $(3, 8, 9)$. We have successively

$$a_3 \geqslant r = \left[\frac{8}{3} \right] = 2 \qquad \text{remainder} = 2$$

$$a_2 = \left[\frac{3}{2} \right] = 1 \qquad \text{remainder} = 1$$

$$a_1 = \left[\frac{2}{1} \right] = 2 \qquad \text{remainder} = 0 .$$

The explicit form of $(3, 8, 9)$ is shown in figure 14. One can check there that div $(3, 8, 9) \subset \left[0, \frac{1}{2} \right]$ because points, $(0, 1, 2)$ are ordered according to the chosen orientation. Moreover, according to proposition 6

$$\text{div } (3, 8, 9) = \left] \frac{1}{3}, \frac{3}{8} \right[. \tag{49}$$

It is obvious that

$$\text{div } (8, 3, 9) = \left] \frac{5}{8}, \frac{2}{3} \right[. \tag{50}$$
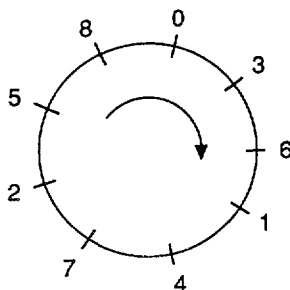

Fig. 14. — Angular permutation characterized by the triple $(3, 8, 9)$.

More generally, by modifying the algorithm of division in the case where $a_1 = 1$, we obtain

Proposition 7 :

If $\qquad$ div $(\alpha, \beta, n) =]\theta_1, \theta_2[= [a_1, a_2, . . , a_{m+1}, r +] \subset \left[0, \frac{1}{2} \right]$

then

$\qquad$ div $(\beta, \alpha, n) =]1 - \theta_2, 1 - \theta_1[= [1, a_1 - 1, a_2, . . , a_{m+1}, r +]$.

The only point which requires a comment concerns the fact that now $a_1 = 1$.

Then $q_0 = q_1 = 1$ and the relation $q_{m-1} < q_m$ is not true for $m = 1$. Hence

$$a_{m+1} \neq \left[\frac{q_{m+1}}{q_m} \right] \qquad (m = 1) . \tag{51}$$

We then stop the algorithm when the remainder vanishes :

$$a_2' = \left[\frac{q_2}{q_1} \right] \qquad \text{(remainder} = 0)$$

and put

$$a_2 = q_2 - 1 = a_2' - 1 \geqslant 1 . \tag{52}$$

3.2.2 *Regular and singular descent.* — Proposition 6 shows that div (α, β, n) depends only on α and β. As a consequence, in the tree of angular permutations, the interval of compatible divergences is modified only on the points of bifurcation, i.e. for the values of n satisfying

$$n = \alpha + \beta . \tag{53}$$

Let us start with a permutation $(\alpha, \beta, n = \alpha + \beta)$ and assume (43) to hold, together with $\alpha < \beta$.
We distinguish between two descents :

1. *Regular descent* ([9]) $(\alpha, \beta, n) \rightarrow (n, \beta, n + 1)$.
Before the transition, $\alpha = q_{m+1} < q_{m, r} = \beta$ $(1 \leqslant r \leqslant a_{m+2})$ (see (32)). After the transition, the only possibility is $n = q_{m+1, s} > q_{m+2} = \beta$ $(1 \leqslant s \leqslant a_{m+3})$. Actually, β, being smaller, must correspond to a principal convergent. Now the transition selects a subset of div (α, β, n) as a new set of compatible divergences [28] :

$$\text{div } (n, \beta, n + 1) \subset \text{div } (\alpha, \beta, n) . \tag{54}$$

This subset is easily computed, since

$$q_{m+2} = q_{m, r} \tag{55}$$

which implies

$$r = a_{m+2} \tag{56}$$

and

$$n = \alpha + \beta = q_{m+1} + q_{m+2} = q_{m+1, 1} . \tag{57}$$

The new set of compatible divergences is given by

$$\text{div } (n, \beta, n + 1) = [a_1, . \ . \ , a_{m+1}, a_{m+2}, 1 +] . \tag{58}$$

2. *Singular descent* $(\alpha, \beta, n) \rightarrow (\alpha, n, n + 1)$.
Now we have $\alpha = q_{m+1} < n = \alpha + \beta = q_{m+1} + q_{m, r} = q_{m, r+1}$. Notice that

$$r < a_{m+2} . \tag{59}$$

Otherwise (32) would not be satisfied. The new interval of compatible divergences reads

$$\text{div } (\alpha, n, n + 1) = [a_1, . \ . \ , a_{m+1}, (r + 1) +] . \tag{60}$$

Note that the regular descent sets $r = 1$, and thus leads to irrationals « slowly approximable » by rationals. An infinite succession of regular transitions leads to a noble number.
Interestingly, the concepts of regular and singular descents correspond to the concepts of regular and singular transitions which have been introduced in the second paper mentioned in

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([9]) The case considered here corresponds to $\alpha < \beta$. If $\alpha > \beta$, then $(\alpha, \beta, n) \rightarrow (\alpha, n, n + 1)$.

[10]. In this reference, self-similar patterns of tangent circles aligned along a logarithmic spiral have been studied. By varying steadily the parameters of the pattern, one can transform a lattice where each circle is tangent with four neighbours into a close-packed lattice where each circle is in contact with six neighbours. Now, one of the parameters happens to be a divergence ; from the close-packed lattice, there are two possibilities to modify the lattice continuously. Their effects on the development of the divergence as a continued fraction are exactly the same as shown by equations (58) and (60). This justifies the names chosen for the two types of descents. Moreover, it was first shown by Levitov that in a system described by a potential energy the regular transitions are favoured [29].

3.2.3 Farey tree structure.

— Let us consider an angular permutation at a bifurcation point. The associate set of compatible divergences is written

$$\text{div} \, (\alpha, \beta, \alpha + \beta) =]\theta_1, \theta_2[= [a_1, . \, . \, , a_{m+1}, r + \,] . \tag{61}$$

The end points $\theta_i \, (i = 1, 2)$ of the interval are given by (46) or (47) according to the parity of m. In any case θ_i is a rational fraction, $\dfrac{p_i}{q_i}$ If we write

$$\theta' = [a_1, . \, . \, , a_{m+1}, r + 1] \tag{62}$$

then, after the bifurcation, each branch will be associated with one of the intervals $]\theta_1, \theta'[$ and $]\theta', \theta_2[$. Now θ' is easily obtained from θ_1 and θ_2

$$\theta' = \frac{p_{m, r+1}}{q_{m, r+1}} = \frac{p_{m, r} + p_{m+1}}{q_{m, r} + q_{m+1}} = \frac{p_1 + p_2}{q_1 + q_2} \tag{63}$$

This is exactly the rule used in the construction of the Farey tree [28, 30]. Figure 15 shows the Farey tree for all angular permutations P_n such that $3 \leq n \leq 7$, together with the corresponding intervals of compatible divergences.

Accordingly we can index uniquely permutations $(\alpha, \beta, \alpha + \beta)$ with the rational numbers $\theta' = \dfrac{p}{q}$ with $(p, q) = 1$ and $q = \alpha + \beta$. We can in particular obtain the permutation $(\alpha, \beta, \alpha + \beta)$ by building the realization $T_q \left(\dfrac{p}{q} \right)$ which takes the form

$$\{C_i \, \theta'\} = \frac{i}{q} \tag{64}$$

whence

$$C_p = 1 . \tag{65}$$

This result, which is rather intuitive, can be obtained from Lemma B.1 and Lemma B.2 (Appendix B). It will be used in section 5 and in Appendix D.

3.3 THE ALGORITHM A AND THE GOLDEN DIVERGENCE.

— We have now achieved a complete knowledge about the construction of angular permutations, for any value of their divergence.

Within this frame it is possible to analyse the algorithm A we have introduced in 1.2.2 to simulate Thornley's dynamic scheme.

We want to show that A corresponds to the algorithm of angular descent with only regular bifurcations, and thus leads to the golden divergence θ_F.
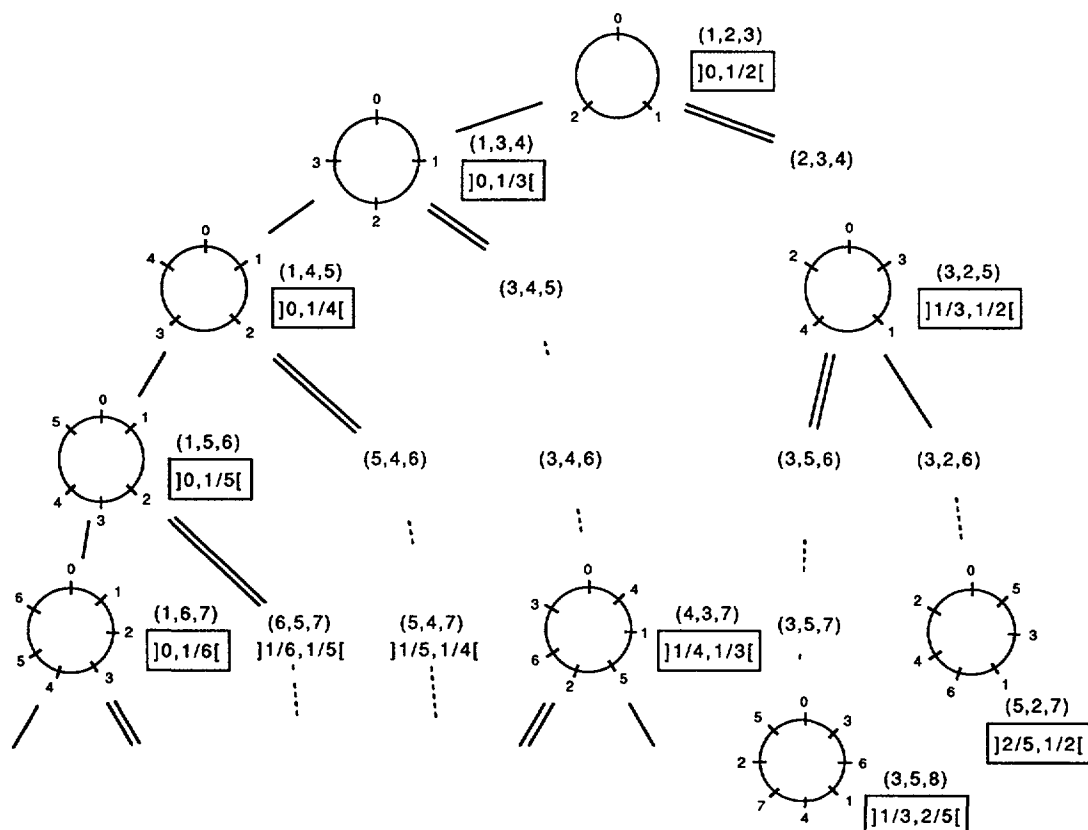
Fig. 15. — The Farey tree of the angular descent of permutation (1, 2, 3). Only the maximal permutations (defined through $(\alpha, \beta, \alpha + \beta)$) have been explicitely represented. Apart from the label (α, β, n), the interval of compatible divergences $]\theta_1, \theta_2[$ is shown. A regular (singular) transition is labelled with a double (single) line. A broken line indicates an angular descent.

Consider a permutation $(\alpha, \beta, n = \alpha + \beta)$ with $\alpha < \beta$. Its regular descent includes the permutation :

$$P_{n'} = (\alpha' = \alpha + \beta, \beta, n' = \alpha' + \beta)$$

(see Fig. 16).

Figure 17 shows the neighbourhood of a point $k \in \{1, 2, ..., \beta - 1\}$ on $P_{n'}$; its construction follows directly from proposition 2 and from the fact that only two differences (namely α' and $-\beta$) can occur in $P_{n'}$, since $n' = \alpha' + \beta$.

Each point $\alpha' + k$ ($k = 1, 2, . , \beta - 1$) has thus been placed between k and its older neighbour, that is $k + \alpha$.

Now this is exactly the rule defined by A, if we consider locating α' between 0 and α as the initial step in the application of A.

Moreover A will locate $\alpha' + \beta$ between β and its older neighbour which is 0 : this demonstrates that A corresponds to the algorithm of regular descent.
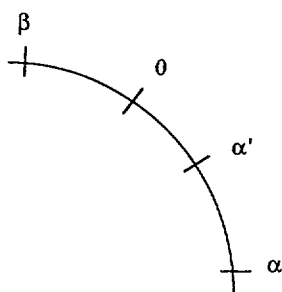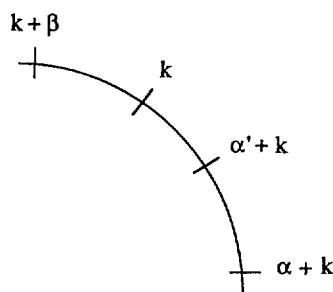
Fig. 16.

Fig. 17.

Fig. 16. — Permutation $P_{n'}$ belonging to the regular descent of permutation $(\alpha, \beta, n = \alpha + \beta)$: see section 3.3.

Fig. 17. — Neighbourhood of a point on $P_{n'}$ (see Sect. 3.3).

4. Stationary permutations.

We have considered so far an evolution law for permutations that does not allow for the description of a steady regime : the state of the apical ring is indeed represented at any time n by a permutation P_n that takes into account the n-sprouts that have appeared during the growth.

But one can also describe a stationary regime in the permutation language.

We introduce the following definitions. Using a similar notation as in section 3.1, we define a permutation $P_n^{(0)}$ obtained from P_n by removing point $0 = C_0$. For convenience, we further subtract one to each of the remaining integers $C_k (1 \leq k \leq n - 1)$ and finally permute them circularly so that the image of 0 through $P_n^{(0)}$ remains 0.

$$P_n = \begin{pmatrix} 0 & 1 & 2 .. & k-1 & k & k+1 & n-1 \\ C_0 = 0 & C_1 & C_2 & C_{k-1} & C_k = 1 & C_{k+1} & . & C_{n-1} \end{pmatrix} \Rightarrow$$

$$P_n^{(0)} = \begin{pmatrix} 0 & 1 & 2 & n-2 \\ 0 & C_{k+1} - 1 & C_{k+2} - 1 & . & C_{k-1} - 1 \end{pmatrix}. \quad (66)$$

As is the case for $P_n^{(n-1)}$, $P_n^{(0)}$ is still a permutation of the first $n - 1$ non negative integers leaving 0 unchanged. We are now able to give a further definition :

P_n is a *stationary permutation* if there exists a permutation $P_{n+1} \in D(P_n)$ such that $P_{n+1}^{(0)} = P_n$.

Clearly a stationary permutation describes a system with a finite memory (the oldest sprouts are forgotten), whose state is invariant under the evolution.

The following proposition states that such permutations necessarily correspond to « phyllotactic » systems, that is, to systems which exhibit a divergence (there is an intuitive reason for this : the concentration field on the apical ring is described by the same permutation if, and only if, it undergoes a mere rotation at each step of the growth process ; the angle characterizing this rotation is nothing but the divergence).

Proposition 8 :

A permutation P_n is stationary if, and only if, it is angular.

The complete proof can be found in Appendix C, and an example is given in figure 18.

Moreover, proposition 8 gives an interesting characterization of angular permutations which involves no arithmetics in contrast to proposition 2.
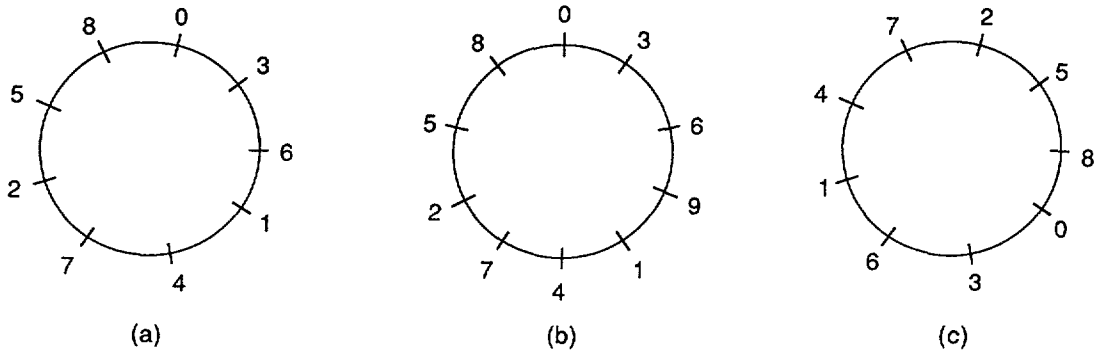
Fig. 18. — An angular permutation is stationary. a) The angular permutation (3, 8, 9). b) The new point 9 has been added to (3, 8, 9) according to the algorithm of angular descent, giving birth to the new angular permutation (3, 8, 10). c) Point 0 has been removed and all other points C_i have been replaced by $C_i - 1$ $(1 \leq i \leq 8)$. The resulting permutation P_9 identifies with (3, 8, 9).

5. Group structure.

5.1 MAXIMAL PERMUTATIONS. — In this section, we analyse some group properties of the angular permutations introduced above.

According to proposition 3, given (α, β), the maximal value q can assume for $P_q = (\alpha, \beta, q)$ to remain angular is given by $\alpha + \beta$. We call *maximal* such a permutation [28, 30].

On the tree of angular permutations, a maximal permutation always corresponds to a bifurcation. Let us define

$$\Omega_q = \{\Pi_\alpha = (\alpha, \beta, \alpha + \beta = q)\} \tag{67}$$

Ω_q is the set of all maximal permutations $\Pi_\alpha = (\alpha, \beta, \alpha + \beta = q)$ of q elements. Given q, Π_α only depends on α which must satisfy

$$(\alpha, q) = 1 \tag{68}$$

(α is not assumed to be $< \beta$ here).

Moreover, a maximal permutation is characterized by the occurrence of only two differences $C_{i+1} - C_i$ $(i = 0, 1, \ldots n - 1)$, as has been mentioned in section 2.3.1. Before giving an explicit description of the structure of Ω_q, we shall introduce two useful notations. Note that q is considered as a fixed integer in what follows.

First, we recall section 3.2.3 : to any $\Pi_\alpha \in \Omega_q$, one can associate the rational $\theta' = \dfrac{p}{q}$, with $(p, q) = 1$. Since q is fixed, we can write $p = p(\alpha)$. Notice that both p and α belong to $\Phi(q)$, the set of positive integers smaller than q and coprime with it.

We shall denote by $R_q(i)$ the rest of the division of integer i through q. The following properties of $R_q(i)$ are straightforward :

$$\begin{aligned} R_q(R_q(i) + R_q(j)) &= R_q(i + j) \\ R_q(i R_q(j)) &= R_q(ij) . \end{aligned} \tag{69}$$

They are valid for any couple (i, j) of integers.

We are now able to state

Proposition 9 :

The set Ω_q, together with the usual composition law of permutations, is a group.
The following identities hold for any Π_α, $\Pi_{\alpha'} \in \Omega_q$

$$\Pi_\alpha(i) = R_q(i\,\alpha) \qquad (1 \le i \le q - 1) \tag{70}$$

$$\Pi_\alpha \cdot \Pi_{\alpha'} = \Pi_{R_q(\alpha\alpha')} \tag{71}$$

$$\Pi_\alpha^{-1} = \Pi_{p(\alpha)} \, . \tag{72}$$

A demonstration of proposition 9 can be found in Appendix D. Note that Ω_q is nothing else than the group of the units of Z_q, the ring of integers modulo q [31].

Angular permutations which are not maximal. — One cannot extend the group structure to angular permutations which are not maximal. Consider for instance permutation $(5, 4, 7)$. According to the algorithm of angular descent, it has to be written as

$$(5, 4, 7) = \begin{pmatrix} 0 & 1 & 2 & 3 & 4 & 5 & 6 \\ 0 & 5 & 1 & 6 & 2 & 3 & 4 \end{pmatrix} = \Pi_5 \, . \tag{73}$$

Now

$$(\Pi_5)^{-1} = \begin{pmatrix} 0 & 1 & 2 & 3 & 4 & 5 & 6 \\ 0 & 2 & 4 & 5 & 6 & 1 & 3 \end{pmatrix} \tag{74}$$

does not satisfy the requirements of proposition 2 and, therefore, cannot be angular.

6. Bijugate phyllotaxis.

6.1 BIJUGATE PATTERN AND SYMMETRIC PERMUTATIONS. — There are two common exceptions to the rule of Fibonacci numbers for parastichies. One finds phyllotactic patterns whose parastichy numbers are either two consecutive numbers of the Lucas series (see Sect. 2.1.1) or of the sequence built up with the double Fibonacci numbers :

$$2 \quad 4 \quad 6 \quad 10 \quad 16 \quad 26\ ..$$

Such patterns are called bijugate. Trijugate (or more generally m-jugate) patterns may also be encountered.

The simplest geometrical model of such a m-jugate pattern is obtained by juxtaposition of m identical strips b_L of a $W_{nm}(\theta)$ lattice, where θ is the golden mean [10].

It is quite improbable that m-jugate patterns are produced by simultaneous appearance of m sprouts on the apical ring, at each step of the growth process. Such a long-ranged correlation in the system would in fact yield a mechanism quite different from the one sketched in 1.2.1 ; in this case, the occurrence of m-jugate patterns would not be exceptional ([10]).

This remark imposes a slight modification in our ideal geometrical model : we may for example associate a different age to each of the m strips b_L, so that at each time n corresponds the birth of a unique sprout n.

The permutation describing such a pattern is obtained by application of the cut-and-projection method we have discussed in 2.2 to our geometrical picture.

([10]) We don't consider here plants that systematically exhibit m-jugate phyllotaxis.

The state of the apical ring at time n would thus be modelled by the following permutation (we consider n even and a bijugate Fibonacci pattern in order to simplify) :

$$P_n = \begin{pmatrix} 0 & 1 & p & p+1 & . & \frac{n}{2}+p & \frac{n}{2}+p+1 & . & n-1 \\ C_0^1 & C_1^1 & . & C_p^1 & C_{p+1}^2 & . & C_{n/2-1}^2 \, C_0^2 \, C_1^2 & . & C_p^2 & C_{p+1}^1 & C_{n/2-1}^1 \end{pmatrix} \quad (75)$$

where C_i^1 is even for all i,

$$C_0^1 = 0 ,$$
$$C_i^2 = C_i^1 + 1 \qquad \text{for all} \qquad i$$

and where

$$\tilde{P}_{\frac{n}{2}} = \begin{pmatrix} 0 & 1 & . & \frac{n}{2}-1 \\ 0 & \dfrac{C_1^1}{2} & & \dfrac{C_{n/2-1}^1}{2} \end{pmatrix} \quad (76)$$

is an angular permutation.

We will say that P_n is *2-symmetric*.

In our case (bijugate Fibonacci pattern), we have : $\theta_F \in \text{div}\,(P_n)$, in other words

$$\frac{C_1^1}{2} \qquad \text{and} \qquad \frac{C_{n/2-1}^1}{2}$$

are two successive Fibonacci numbers.

6.2 SYMMETRIC PERMUTATIONS AND PERTURBED DYNAMICS. — Surprisingly, the algorithm A generates such abnormal permutations when an error occurs in an initial step. Consider for example the irregular permutation P_5 (Fig. 19).

If A had been correctly applied, 4 would have been placed between 1 and 2. Now suppose that we go on and apply A to P_5. As 4 has been placed next to 0, 5 is put between 1 and its older neighbour, that is 2, and so on. We obtain at time 19 a permutation whose circular representation is in figure 20.
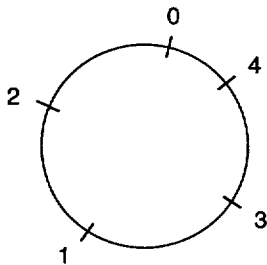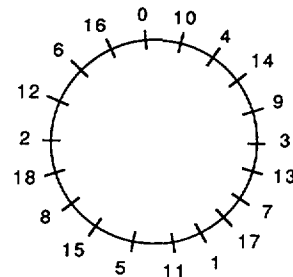

Fig. 19.   Fig. 20.

Fig. 19. — An error occurred in step 4.

Fig. 20. — A permutation with a symmetry of order 2 is obtained as the result of one initial error.

It is easy to check that P_{19} satisfies all the properties stated above of a 2-symmetric permutation.

More generally, if A is applied (with a convenient choice of the initial step) to an m-symmetric permutation, then the permutation remains m-symmetric and its divergence tends towards a noble number.

This result shows that A is more than a simple transcription of the algorithm of regular descent, whose construction relies on purely mathematical considerations.

In this sense A may be considered as an equivalent of Thornley's dynamic scheme for permutations.

7. Conclusions.

Following reference [18], we tried in this paper to introduce a temporal factor into phyllotaxis. In reference [14], a kinetic equation describes the evolution of the concentration of an inhibitor on the apical ring where the new shoots of a phyllotactic structure appear. « Inhibitor » is the name given to some morphogen, an hypothetical chemical substance assumed to preclude the immediate emergence of a new sprout. Each new-born shoot is supposed to be followed by a local increase of inhibitor concentration which soon fades away through diffusion and degradation. As a consequence, the overall concentration profile of inhibitor shows various peaks more or less sharp according to the order of birth of each shoot, assumed to appear in succession.

Our aim was to analyze the algebraic structure of a distribution of a finite number of points on a circle together with their temporal evolution. The points on the circle are assumed to correspond to the distribution of peaks on the apical ring. We have been able to put forward a system of regular and singular transitions between permutations. This system builds a hierarchical structure similar to the classification of the transitions observed between lattices of tangent circles alined along equiangular spirals or helices [32, 10]. As a consequence, the special role of the noble numbers as divergences can be emphasized.

The structure of this algebraic model is general enough so that it is not necessarily related to a chemical model. In fact, many biologists look for a relation between the phyllotactic structure and the existence of a morphogen. Now our paper shows that, as one could expect, the general occurrence of certain noble divergences is unlikely to give any information over the chemical processes ruling the appearance of new shoots. More precisely, if this kind of information could be drawn from a phyllotactic structure, it ought to be looked for in anomalous patterns, for instance in structures characterized by a Lucas divergence, or in the case of m-jugate phyllotaxis.

The fact that the same hierarchical structure (i.e. a Farey-tree) emerges both from a pure static analysis and from a model of the process of morphogenesis is not so astonishing, after all. It is the consequence of the fact that the pattern, during its growth, builds its scaffolding, which is nothing else than its proper structure.

Another conclusion can be drawn from this study. A large majority of botanical patterns one meets belong to the golden phyllotaxis (their divergence is close to the golden mean), while a small proportion of spiral patterns show the Lucas divergence. Moreover, there are still less frequent values of the observed divergence, together with more complicated patterns, for instance those which put forth both an axis of rotation and a spiralled lattice. Observing the Farey-tree which emerges from this morphogenetic study now suggests that the possible random fluctuation responsible for any anomalous structure (i.e. different from the golden one), if there is any, must occur very early during the morphogenetic process. In the absence of such a fluctuation, the only possible transitions seem to correspond to less important

bifurcations leaving the value of the divergence almost unchanged. In fact, analyzing these assumed fluctuations could then lead into the core of a possible chemical process.

Acknowledgments.

Appendix A.

In order to prove proposition 1, we first demonstrate the two following lemmas.

Lemma A.1.

Let $V = \{n\mathbf{a} + m\mathbf{b} \; ; \; n, m \in \mathbf{Z}\}$ be a lattice in $\mathbf{R}^2$. If the basis vectors $\mathbf{a}$ and $\mathbf{b}$ have slopes of opposite signs, then they belong to the convex envelopes P_+ and P_- of the lattice.

Proof.

We prove it graphically. First observe that the unit cell defined by $\mathbf{a}$ and $\mathbf{b}$ contains no lattice point, whatever their respective slopes (see Fig. A1). From this follows that the open set Ω bounded by the lines $k\mathbf{b}$ and $k\mathbf{b} + \mathbf{a}$, $k \in \mathbf{R}$, contains no lattice point (Fig. A2). If $\mathbf{a}$ and $\mathbf{b}$ have slopes of opposite signs, we define $\Omega' = \Omega \cap \mathbf{R}_+ \times \mathbf{R}_+$ (Fig. A3).

Now if the convex envelope P_+ does not contain $\mathbf{a}$, it must cut the vector $\mathbf{a}$ (to envelop the point a), be a segment in Ω' (if it was a broken line, the angle would imply the existence of a lattice point in Ω'). Moreover it cannot cross the x- or y-axes in Ω' · this is impossible, consequently P_+ contains $\mathbf{a}$. The case of vector $\mathbf{b}$ is similar.

Lemma A.2 (For a definition of a $W_{nm}(\theta)$-lattice, see Sect. 2.2.1).

Consider a $W_{nm}(\theta)$-lattice. If $\mathbf{W}_{nm}$ and $\mathbf{W}_{n'm'}$ are basis vectors with slopes of opposite signs, and if $n > 0$, $n' > 0$, then $\mathbf{W}_{n+n', m+m'}$ belongs to P_- or P_+ ; moreover there is no point W_{ij} on P_- or P_+ with max $[n, n'] < i < n + n'$.
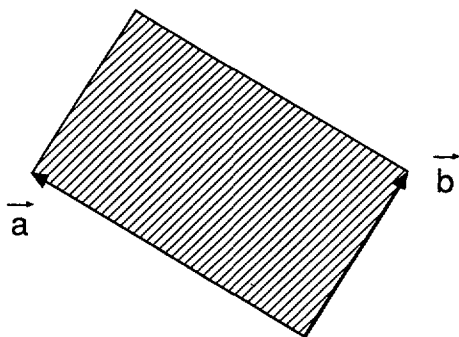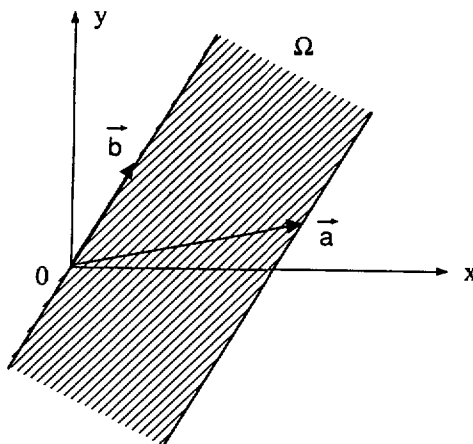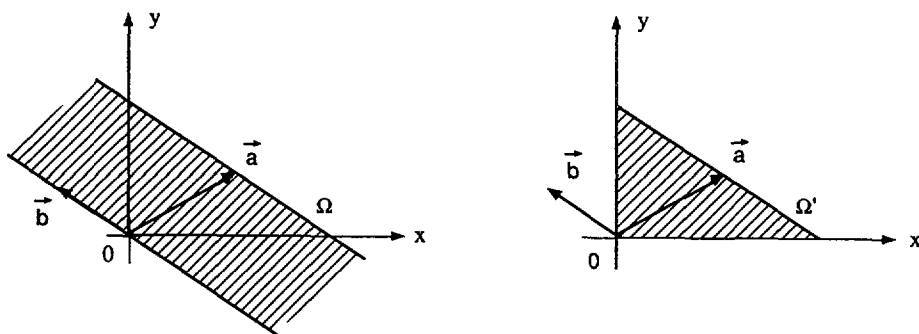

Fig. A1.

Fig. A2.

Fig. A3.

Proof.

Simply consider the diagram in figure A4. The hatched zone contains no lattice point, since the unit cell defined by $\mathbf{W}_{nm}$ and $\mathbf{W}_{n'm'}$ is empty. Hence $\mathbf{W}_{nm}$ and $\mathbf{W}_{n'm'}$ are basis vectors, as well as $\mathbf{W}_{n'm'}$ and $\mathbf{W}_{n+n',m+m'}$. Lemma A.1 then shows that $\mathbf{W}_{n+n',m+m'}$ necessarily belongs to P_- or P_+.

Lemma A.1 also implies that $\mathbf{W}_{nm} \in P_-$ and $\mathbf{W}_{n'm'} \in P_+$ (we consider the case of Fig. A4). It is then clear that a point $\mathbf{W}_{ij}$ for which max $[n, n'] < i < n + n'$ belongs to a convex envelope only if it is in the hatched zone : this is of course impossible. We then have
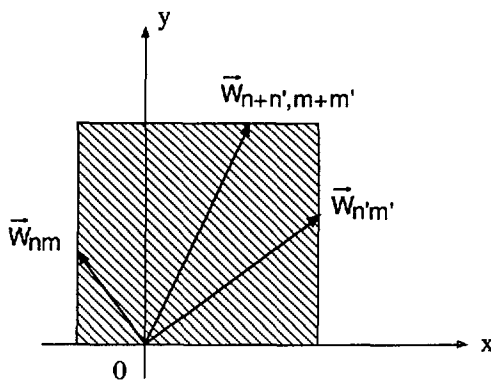

Fig. A4.

Proposition 1 (Sect. 2.2.3).

In a $\mathrm{W}_{nm}(\theta)$*-lattice,* P_- *(resp.* P_+*) goes through points*

$$\mathbf{W}_{q_{n,r}p_{n,r}} (1 \leqslant r \leqslant a_{n+2})$$

n being odd (resp. even).

Proof.

First notice that

$$q_{n,r}\, \theta - p_{n,r} > 0 \qquad \text{if} \qquad n \text{ is even}$$
$$q_{n,r}\, \theta - p_{n,r} < 0 \qquad \text{if} \qquad n \text{ is odd}.$$

Hence

$$\mathbf{W}_{q_{n,r}p_{n,r}} \in R_+ \times R_+ \qquad \text{if} \qquad n \text{ is even}$$
$$\mathbf{W}_{q_{n,r}p_{n,r}} \in R_- \times R_+ \qquad \text{if} \qquad n \text{ is odd}. \qquad (A1)$$

Now we demonstrate the proposition by induction.

Suppose that for $i \leq q_{n,r} (1 \leq r \leq a_{n+2})$, the points $\mathbf{W}_{ij}$ that constitute $\mathbf{P}_-$ and $\mathbf{P}_+$ fulfil the requirements of the proposition and suppose further that $\mathbf{W}_{q_{n,r} p_{n,r}}$ and $\mathbf{W}_{q_{n+1} p_{n+1}}$ generate the lattice.

We know then by Lemma A.2 that $\mathbf{W}_{q_{n,r+1} p_{n,r+1}}$ (or $\mathbf{W}_{q_{n+1,1} p_{n+1,1}}$ if $r = a_{n+2}$) is on $\mathbf{P}_-$ or $\mathbf{P}_+$, and that there is no point $\mathbf{W}_{ij}$ on $\mathbf{P}_-$ or $\mathbf{P}_+$ with $q_{n,r} < i < q_{n,r+1}$ $(q_{n,r} < i < q_{n+1,1}$ if $r = a_{n+2})$.

It has also been shown in the proof of Lemma A.2 that $\mathbf{W}_{q_{n,r+1} p_{n,r+1}}$ and $\mathbf{W}_{q_{n+1} p_{n+1}}$ (or $\mathbf{W}_{q_{n+2} p_{n+2}}$ and $\mathbf{W}_{q_{n+1,1} p_{n+1,1}}$ if $r = a_{n+2}$) generate the lattice ; thus the induction hypothesis is verified for $i \leq q_{n,r+1}$ (or $i \leq q_{n+1,1}$ if $r = a_{n+2}$).

To close the demonstration, we simply have to prove that $\mathbf{W}_{q_0 p_0}$ and $\mathbf{W}_{q_1 p_1}$ generate the lattice (we know by Lemma 1 that these points are on $\mathbf{P}_-$ and $\mathbf{P}_+$ if this condition is satisfied). But $\forall n,\ m \in \mathbb{Z}$, we can write

$$\begin{aligned}
\mathbf{W}_{nm} &= (n - ma_1)\,\mathbf{W}_{10} + m\mathbf{W}_{a_1 1} \\
&= (n - ma_1)\,\mathbf{W}_{q_0 p_0} + m\mathbf{W}_{q_1 p_1}\,.
\end{aligned} \tag{A2}$$

Appendix B.

In the text we have outlined the idea of the cut-and-projection method (chapter 2.2), which allows proposition 2 to be proven. Here we give the details of the method.

Definition : the neighbouring points $\mathbf{A}^L_{nm}$ and $\mathbf{B}^L_{nm}$ of the point $\mathbf{W}_{nm}$ in the strip $\overline{b}_L$ are the only points in $\overline{b}_L$ whose projection on the x-axis is next to the projection of $\mathbf{W}_{nm}$; the projection of $\mathbf{A}^L_{nm}$ will be taken on the left of the projection of $\mathbf{B}^L_{nm}$. We simply write $\mathbf{A}^L_n$ and $\mathbf{B}^L_n$ for the neighbours of a point $\mathbf{W}_n$.

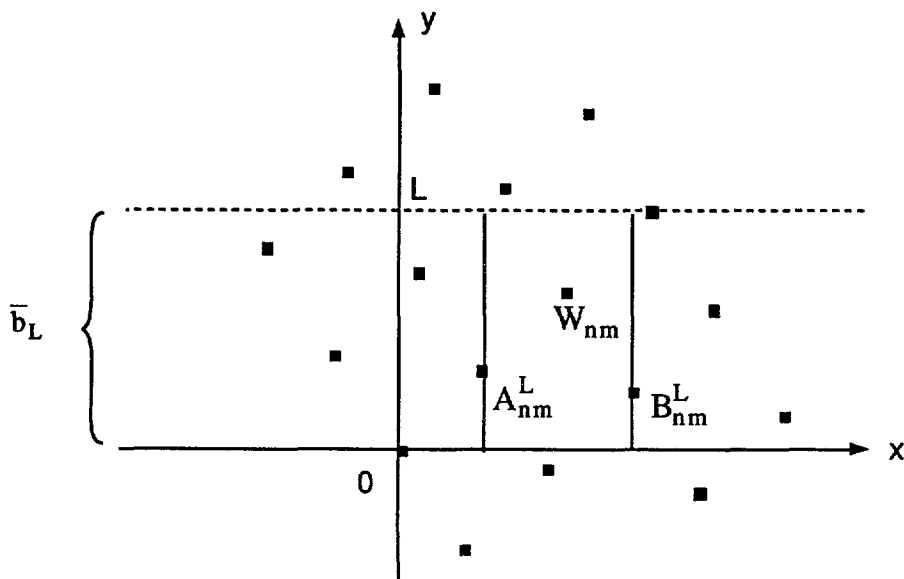Figure B1 illustrates this definition.

Fig. B1.

Lemma B.1.

Let $\bar{b}_L$ be a lattice strip in a $W_{nm}(\theta)$-lattice, with $L \in \{q_{n,r}; \quad q_{n,r} + 1; \ . \ ; q_{n,r} + q_{n+1} - 1\}$, $n \geq 0$ and $1 \leq r \leq a_{n+2}$.
We have

$$A_0^L = W_{q_{n+1}p_{n+1}} \quad and \quad B_0^L = W_{q_{n,r}p_{n,r}} \quad if \ n \ is \ even$$
$$A_0^L = W_{q_{n,r}p_{n,r}} \quad and \quad B_0^L = W_{q_{n+1}p_{n+1}} \quad if \ n \ is \ odd. \tag{B1}$$

Moreover A_0^L and B_0^L are basis vectors of the $W_{nm}(\theta)$-lattice.

Proof.

If A_0^L and B_0^L are neighbouring points of the origin, then they have slopes of opposite signs and they generate the lattice, since they define an empty cell (Fig. B2).
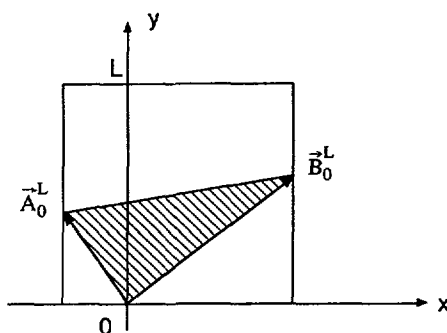

Fig. B2. — By definition of A_0^L and B_0^L, the hatched zone contains no lattice point.

We can therefore apply Lemma A.1. Since $L > q_1$, we can write

$$A_0^L = W_{q_{h,i}p_{h,i}} \quad and \quad B_0^L = W_{q_{j,k}p_{j,k}} \tag{B2}$$

with $1 \leq i \leq a_{h+2}$ and $1 \leq k \leq a_{j+2}$.

We now consider the case of even n. Since $W_{q_{h,i}p_{h,i}}$ and $W_{q_{j,k}p_{j,k}}$ are the neighbouring points of 0 in $\bar{b}_L$, $q_{j,k}$ is the greatest denominator of convergent with even j which is less than L.

Now

$$q_{n,r} \leq L$$
$$q_{n,r+1} = q_{n,r} + q_{n+1} > L \tag{B3}$$

so that $q_{j,k} = q_{n,r}$, since n is even. Similarly, $q_{h,i}$ is the greatest denominator of convergent with odd h which is less than L.

Now

$$q_{n+1} < q_{n+1} + q_n = q_{n,1} \leq L$$
$$q_{n+1,1} = q_{n+1} + q_{n+2} > q_{n+1} + q_{n,r} - 1 \geq L \tag{B4}$$

so that $q_{h,i} = q_{n+1}$, since $n + 1$ is odd.

Lemma B.2.

Let $\bar{b}_L$ be any strip in a $W_{nm}(\theta)$-lattice, and let W_{nm} be a point in $\bar{b}_L$. Then we have

*• If $L \in \{q_{k,r} ; q_{k,r} + 1 ; ... ; q_{k,r} + q_{k+1} - 1\}$, then $A_{nm}^L - W_{nm}$ is necessarily equal to one of the vectors $\{A_0^L ; -B_0^L ; A_0^L - B_0^L\}$
and is never equal to the third one if and only if*

$$L = q_{k,r} + q_{k+1} - 1 .$$

• If $L < q_1$, $A_{nm}^L - W_{nm}$ is necessarily equal to one of the vectors $\{W_{L1} ; -W_{10}\}$.

Proof.

FIRST CASE : $L \geq q_1$. — Let us define the following sets

$$\Omega = W_{nm}(\theta) \cap R \times [n - q_{k,r} - q_{k+1} + 1, n + q_{k,r} + q_{k+1} - 1]$$
$$\Omega_+ = W_{nm}(\theta) \cap R \times [n, n + q_{k,r} + q_{k+1} - 1] \qquad (B5)$$
$$\Omega_- = W_{nm}(\theta) \cap R \times [n - q_{k,r} - q_{k+1} + 1, n] .$$

We also define

$$A_{\pm} = W_{nm} \pm A_0^L$$
$$B_{\pm} = W_{nm} \pm B_0^L$$
$$C_{\pm} = W_{nm} \pm (A_0^L - B_0^L) . \qquad (B6)$$

It is easy to see that $\bar{b}_L \subset \Omega$ (because $W_{nm} \in \bar{b}_L$ and $L \leq q_{k;r} + q_{k+1} - 1$). One similarly checks that $A_{\pm}$, $B_{\pm}$, $C_{\pm} \in \Omega$; the situation is illustrated in figure B3. Finally, notice that we can define $A_{nm}^{\Omega_{\pm}}$ and $B_{nm}^{\Omega_{\pm}}$ in the same way as we defined A_{nm}^L and B_{nm}^L . we simply substitute $\Omega_{\pm}$ to $\bar{b}_L$ in the definition.
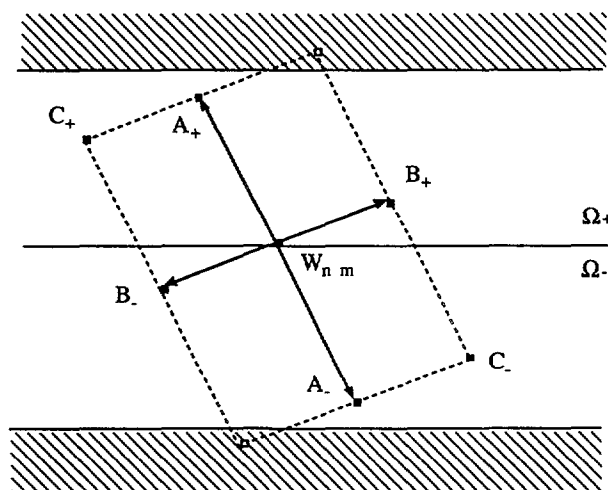

Fig. B3. — The hatched zone and the white points do not belong to Ω.

Now observe that Ω_+ can be obtained by translating $\overline{b}_{q_{k,r}+q_{k+1}-1}$ by the vector $\mathbf{W}_{nm}$; as Lemma B.1 also implies

$$\mathbf{A}_0^{q_{k,r}+q_{k+1}-1} = \mathbf{A}_0^L$$
$$\mathbf{B}_0^{q_{k,r}+q_{k+1}-1} = \mathbf{B}_0^L \tag{B7}$$

we obtain

$$\mathbf{A}_{nm}^{\Omega_+} = \mathbf{A}_0^L + \mathbf{W}_{nm} = \mathbf{A}_+$$
$$\mathbf{B}_{nm}^{\Omega_+} = \mathbf{B}_0^L + \mathbf{W}_{nm} = \mathbf{B}_+ \tag{B8}$$

Ω_- is obtained by inverting $\overline{b}_{q_{k,r}+q_{k+1}-1}$ with respect to the origin and by translating it by the vector $\mathbf{W}_{nm}$. Thus

$$\mathbf{A}_{nm}^{\Omega_-} = \mathbf{B}_-$$
$$\mathbf{B}_{nm}^{\Omega_-} = \mathbf{A}_- \tag{B9}$$

We are interested in $\mathbf{A}_{nm}^L$. Two cases may be considered

• $\left\{\mathbf{A}_{nm}^{\Omega_+}, \mathbf{A}_{nm}^{\Omega_-}\right\} \cap \overline{b}_L \neq \varnothing$.

In this case, since $\overline{b}_L \subset \Omega = \Omega_- \cup \Omega_+$, we have

$$\mathbf{A}_{nm}^L \in \left\{\mathbf{A}_{nm}^{\Omega_+}, \mathbf{A}_{nm}^{\Omega_-}\right\} = \left\{\mathbf{A}_+, \mathbf{B}_-\right\} . \tag{B10}$$

The proposition is then proved.

• $\left\{\mathbf{A}_{nm}^{\Omega_+}, \mathbf{A}_{nm}^{\Omega_-}\right\} \cap \overline{b}_L = \varnothing$.

Figure B4 illustrates the meaning of this relation. Suppose k is odd ; using Lemma B.1 and the definition of $\overline{b}_L$, it is easy to see that the situation of figure B4 is realized if and only if $n + q_{k,r} > L$ and $n - q_{k+1} < 0$. In other words (k is odd)

$$0 \leqslant L - q_{k,r} < n < q_{k+1} . \tag{B11}$$

Similarly, for even k,

$$0 \leqslant L - q_{k+1} < n < q_{k,r} . \tag{B12}$$

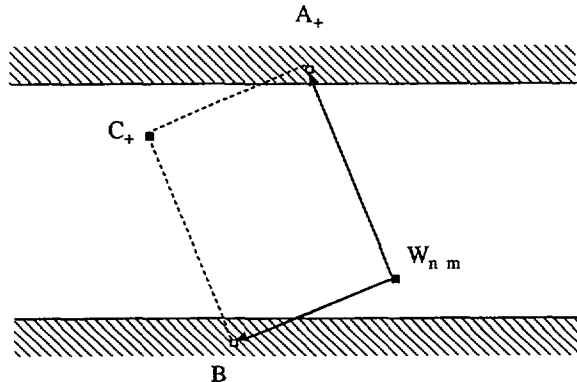Fig. B4. — The hatched zone is out of $\overline{b}_L$.

These inequalities have a solution $n \in N^*$ if and only if $L < q_{k,r} + q_{k+1} - 1$. They also imply

$$0 \leqslant L - q_{k+1} < n + q_{k,r} - q_{k+1} < q_{k,r} \leqslant L \quad \text{for odd } k$$
$$0 \leqslant L - q_{k,r} < n - q_{k,r} + q_{k+1} < q_{k+1} \leqslant L \quad \text{for even } k \tag{B13}$$

i.e. $C_+ \in \bar{b}_L$.

It is then clear in figure B4 that $A_{nm}^L = C_+$ (since A_0^L and B_0^L generate the lattice, the cell defined by $W_{nm} - A_+ - C_+ - B_-$ contains no lattice point). The first part of the proposition is now proved.

SECOND CASE : $L \leqslant q_1$. — It is easy to construct the lattice strip $\bar{b}_L$ with the basis vectors W_{10} and W_{01} (Fig. B5), because $\theta q_1 < 1$ and $W_{10} = (\theta, 1)$. The proposition is obvious in figure B5, as a consequence of the periodicity of the $W_{nm}(\theta)$-lattice.
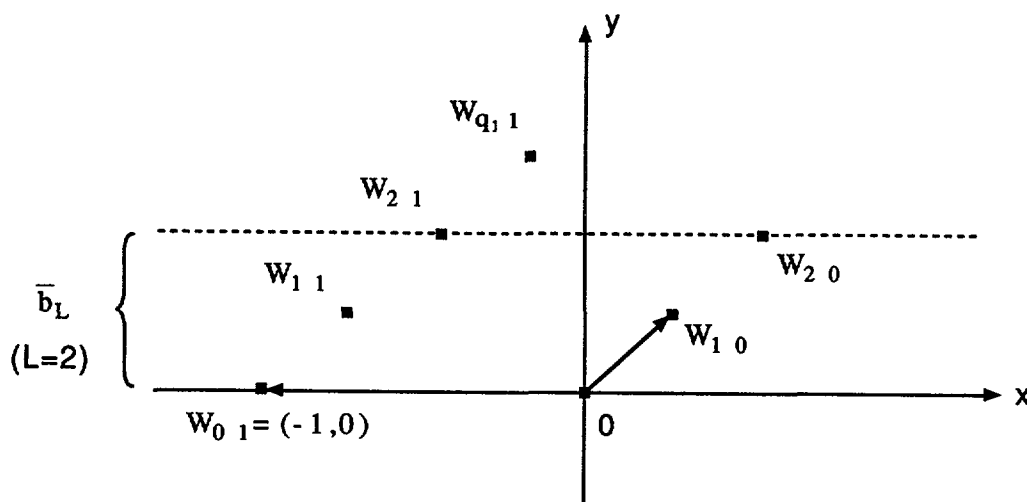

Fig. B5.

Lemma B.3.

Let a_2, b_2 be two positive integers such that $(a_2, b_2) = 1$ and let b_1 be an irrational number in the interval $\left]0, \dfrac{1}{a_2}\right[$. Let us define

$$a_1 = \frac{1 - a_2 b_1}{b_2} > 0 \qquad \mathbf{a} = \begin{pmatrix} a_1 \\ a_2 \end{pmatrix} \qquad \mathbf{b} = \begin{pmatrix} b_1 \\ -b_2 \end{pmatrix} \tag{B14}$$

and $V = \{n\mathbf{a} + m\mathbf{b} ; n, m \in Z\}$.

Then there exists an irrational number $\theta \in]0, 1[$ such that $V = W_{nm}(\theta)$.

Proof.

Since $(a_2, b_2) = 1$, there exists $n, m \in Z$ such that

$$na_2 - mb_2 = 1 . \tag{B15}$$

Moreover $a_1 b_2 + a_2 b_1 = 1$, by construction. Then $\forall k \in Z$, one can construct the vector

$$kb_2\, \mathbf{a} + ka_2\, \mathbf{b} = \mathbf{k} = \begin{pmatrix} k \\ 0 \end{pmatrix}. \tag{B16}$$

Now let n', $m' \in Z$ satisfy (B.15) and $k' \in Z$ satisfy

$$\theta \equiv n'\, a_1 + m'\, b_1 + k' \in \;]0,\, 1[\;.$$

The number θ we have defined is of course irrational, since

$$n'\, a_1 + m'\, b_1 = \frac{n' - b_1}{b_2} \tag{B17}$$

and b_1 is irrational. One easily checks

$$n'\, \mathbf{a} + m'\, \mathbf{b} + \mathbf{k}' = (n' + k'\, b_2)\, \mathbf{a} + (m' + k'\, a_2)\, \mathbf{b} = \begin{pmatrix} \theta \\ 1 \end{pmatrix}. \tag{B18}$$

In other words, we have proved that $\begin{pmatrix} 1 \\ 0 \end{pmatrix} \in V$ and $\begin{pmatrix} \theta \\ 1 \end{pmatrix} \in V$, i.e. $W_{nm}(\theta) \subset V$. The converse is also true, since direct calculation shows that

$$\mathbf{a} = a_2 \begin{pmatrix} \theta \\ 1 \end{pmatrix} - (a_2\, k' + m') \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

$$\mathbf{b} = -b_2 \begin{pmatrix} \theta \\ 1 \end{pmatrix} + (b_2\, k' + n') \begin{pmatrix} 1 \\ 0 \end{pmatrix}. \tag{B19}$$

We now prove

Proposition 2 (Sect. 2.3).

A permutation P_n is angular if and only if the differences

$$C_{i+1} - C_i \qquad i = 0, 1, .\, , n - 1$$

take only two values

$$\alpha \quad and \quad -\beta \qquad (\alpha, \beta \in N^*)$$

and possibly the third value

$$\gamma = \alpha - \beta$$

which can only occur if i is different from 0 or $n - 1$.

Proof.

Suppose P_n is angular and let $\theta \in \;]0,\, 1[$ be a compatible divergence, we choose as irrational to simplify. We can construct a realization $T_n(\theta)$ of P_n by projecting on $[0, 1[$ the strip b_{n-1} of the $W_{nm}(\theta)$-lattice, and by associating the integer i with the projection of W_i; the proposition then directly follows from Lemmas B.1 and B.2.

Conversely, let P_n be a permutation satisfying the conditions of the proposition. We want to show that it is angular by constructing a corresponding $W_{nm}(\theta)$-lattice. To this aim consider the vectors

$$\mathbf{a} = \begin{pmatrix} a_1 \\ \alpha \end{pmatrix} \qquad \mathbf{b} = \begin{pmatrix} b_1 \\ -\beta \end{pmatrix} \tag{B20}$$

where b_1 is an irrational number taken in the interval $]0, 1/\alpha[$ and $a_1 = \dfrac{1 - \alpha b_1}{\beta} > 0$. α and β are coprime, that is

$$(\alpha, \beta) = 1 \tag{B21}$$

since there exists $i \in N_{n-1}$ such that $C_i = 1$, so that

$$1 = C_i = k\alpha + \ell\beta + m\gamma \tag{B22}$$

where $k, \ell, m \in Z$. We can then apply Lemma B.3 : if $V = \{n\mathbf{a} + m\mathbf{b} ; n, m \in Z\}$, then there exists an irrational $\theta \in]0, 1[$ such that $V = W_{nm}(\theta)$.

In order to establish a relation between the lattice points and the integers C_0, $C_1, . , C_{n-1}$, let us construct the vector sequence

$$\mathbf{v}_{i+1} = \begin{cases} \mathbf{a} & \text{if } C_{i+1} - C_i = \alpha \\ \mathbf{b} & \text{if } C_{i+1} - C_i = -\beta \\ \mathbf{a} + \mathbf{b} & \text{if } C_{i+1} - C_i = \gamma \end{cases} \tag{B23}$$

where $i = 0, 1, . , n - 1$. By defining

$$\begin{aligned} \mathbf{C}_0 &= 0 \\ \mathbf{C}_{i+1} &= \mathbf{C}_i + \mathbf{v}_{i+1} \end{aligned} \tag{B24}$$

for $i = 0, 1, ..., n - 1$, one constructs a vector sequence in V and also in $W_{nm}(\theta)$. This sequence has the following property :

$$\mathbf{C}_i = \begin{pmatrix} \cdots \\ C_i \end{pmatrix} . \tag{B25}$$

It constitutes a broken line in the lattice (see for example Fig. B6). The point is now to see that this broken line is confined in $[0, 1] \times R_+$. In this part of the plane, there is in fact no ambiguity if a point W_{nm} is simply written W_n, because of (13) (Sect. 2.2.1). Hence

$$\mathbf{C}_i = \begin{pmatrix} \{C_i \theta\} \\ C_i \end{pmatrix} . \tag{B26}$$

It is then clear that

$$0 = \{C_0 \theta\} < \{C_1 \theta\} < \{C_2 \theta\} < \cdot \quad < \{C_{n-1}\} \tag{B27}$$

which proves that P_n is angular.

Call S the broken line defined by the lattice points $\mathbf{C}_0, \mathbf{C}_1, ..., \mathbf{C}_n$. As a consequence of the properties of the points $\mathbf{C}_i$, it is clear that S ends when it cuts the x-axis. Now we want to show that S is confined in $[0, 1] \times R_+$. Let us prove it by reduction ad absurdum and suppose that S ends over $[0, 1]$ on the x-axis.

Let T be the broken line obtained by shifting the restriction of S to $[0, 1] \times R_+$ by a vector $(1, 0)$. From the periodicity of the $W_{nm}(\theta)$-lattice it follows that T connects lattice points. Figure B7 shows that if S ends in $[1, 2] \times R_+$, it must cut T. Since S and T are constituted by vectors $\mathbf{a}$, $\mathbf{b}$, $\mathbf{a} + \mathbf{b}$ ordered endway and connecting lattice points, S and T cross on a lattice point, say $\mathbf{C}_j = (.. , C_j)$. Now since $\mathbf{C}_j \in T$, there exists $\mathbf{C}_i \in [0, 1] \times R_+$ such that

$$\mathbf{C}_j = \mathbf{C}_i + \begin{pmatrix} 1 \\ 0 \end{pmatrix} = \begin{pmatrix} \cdots \\ C_i \end{pmatrix} \tag{B28}$$
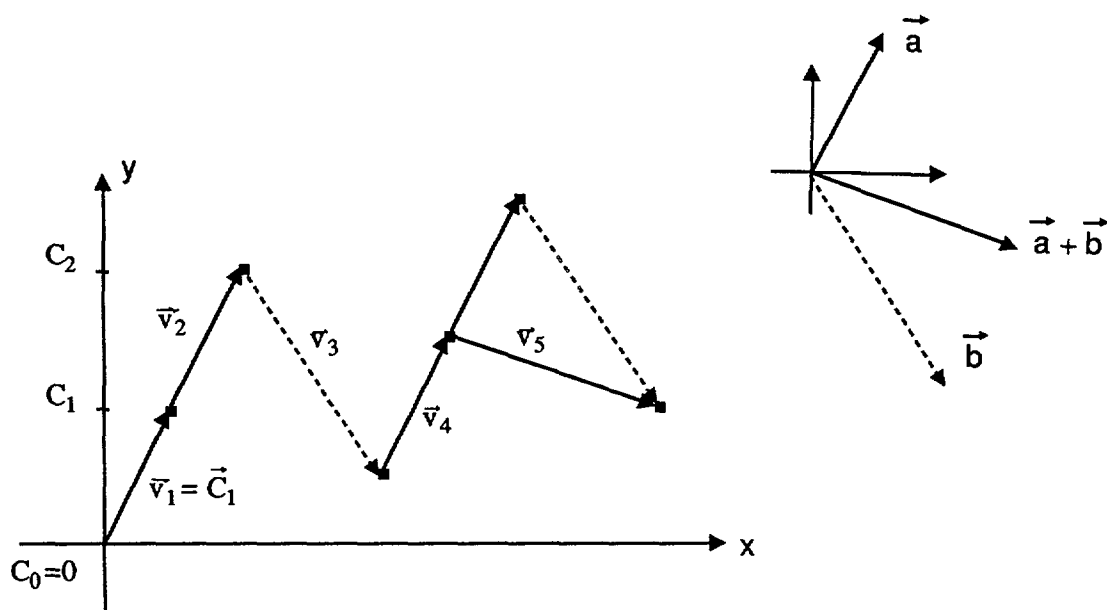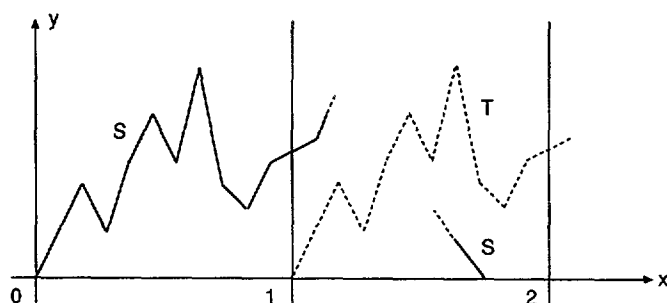
Fig. B6.

Fig. B7.

which is impossible because $C_i \neq C_j$ if $i \neq j$. S cannot therefore end in $[1, 2] \times R_+$. But the same argument can be used in $[2, 3] \times R_+$, and so on ; finally we conclude that S never cuts the x-axis, which is a contradiction.

Let us prove

Proposition 3 (Sect. 2.3.1).

For any triple $(\alpha, \beta, n) \in N^3$ which satisfies the conditions

$$(\alpha, \beta) = 1 \tag{B29}$$
$$\max [\alpha, \beta] + 1 \leq n \leq \alpha + \beta \tag{B30}$$

there exists a unique angular permutation P_n such that

$$C_1 = \alpha \qquad C_{n-1} = \beta .$$

Proof.

Let us first prove the existence of P_n. We define

$$\mathbf{a} = \begin{pmatrix} a_1 \\ \alpha \end{pmatrix} \qquad \mathbf{b} = \begin{pmatrix} -b_1 \\ \beta \end{pmatrix} \tag{B31}$$

where b_1 is an irrational number taken in the interval $]0, 1/\alpha[$ and $a_1 = \dfrac{1 - \alpha b_1}{\beta} > 0$. We know by Lemma B.3 that there exists an irrational $\theta \in]0, 1[$ such that $\{a ; b\}$ generate $W_{nm}(\theta)$. If we consider the strip $\bar{b}_{n-1}$ of this lattice, it is clear that $\mathbf{b} = \mathbf{A}_0^{n-1}$ and $\mathbf{a} = \mathbf{B}_0^{n-1}$ (see Fig. B8). To obtain P_n, simply project this strip on the segment $[0, 1[$, according to the method described at the beginning of the proof of Proposition 2.

Now to see that P_n is unique, notice that in a strip $\bar{b}_{n-1}$ of any $W_{nm}(\theta)$-lattice, the numbers n, i, a_2, b_2 fully determine which one of the vectors

$$\mathbf{A}_0^{n-1} = \begin{pmatrix} a_1 \\ a_2 \end{pmatrix}, \quad \mathbf{B}_0^{n-1} = \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}, \quad \mathbf{A}_0^{n-1} - \mathbf{B}_0^{n-1} \tag{B32}$$

is equal to the difference $\mathbf{A}_{ij}^{n-1} - \mathbf{W}_{ij} \ \forall \mathbf{W}_{ij} \in \bar{b}_{n-1}$ (to prove this, refer to the demonstration of Lemma B.2 : either A_+ or B_-, or neither A_+ nor B_- but C_+ is in $\bar{b}_{n-1}$, and this depends only on the parameters n, i, a_2, b_2).

From thit it follows that the angular permutation defined by the projection of a strip $\bar{b}_{n-1}$ on the x-axis is fully determined by the numbers n, a_2, b_2. Of course, a_2 and b_2 correspond to $C_1 = \alpha$, $C_{n-1} = \beta$.
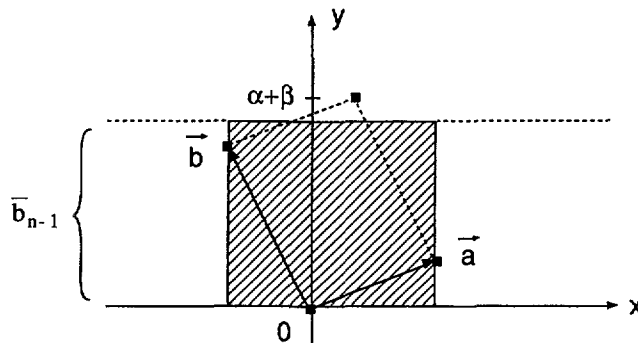

Fig. B8. — The hatched zone contains no lattice point since $\{a ; b\}$ generates $W_{nm}(\theta)$.

Appendix C.

We assume that the reader is familiar with the definitions of the operations $P_{n+1}^{(n)}$ and $P_{n+1}^{(0)}$; each of them produces a new permutation P_n from a given permutation P_{n+1} (cf. 3.1 and 4). Let us introduce for convenience the notation

$$P_{n+1}^{(n)\,(0)} \equiv P_n^{(0)} \qquad \text{where} \qquad P_n = P_{n+1}^{(n)}$$

$$P_{n+1}^{(0)\,(n-1)} \equiv P_n^{(n-1)} \qquad \text{where} \qquad P_n = P_{n+1}^{(0)}.$$
$$\tag{C1}$$

One easily checks that

$$P_{n+1}^{(n)\,(0)} = P_{n+1}^{(0)\,(n-1)} \tag{C2}$$

Lemma C.1.

If P_{n+1} is a stationary permutation, then $P_{n+1}^{(n)} = P_n$ is also stationary.

Proof.

Since P_{n+1} is stationary, there exists $P_{n+2} \in D(P_{n+1})$ such that $P_{n+2}^{(0)} = P_{n+1}$. Now simply consider the properties of P_{n+1}.

- $P_{n+1} \in D(P_n)$.
- $P_{n+1}^{(0)} = P_{n+2}^{(n+1)(0)} = P_{n+2}^{(0)(n)} = P_{n+1}^{(n)} = P_n$.

Lemma C.2.

Let $P_n = (\alpha, \beta, n)$ be an angular permutation. If $P_{n+1} \in D(P_n)$ is stationary, then P_{n+1} is angular.

Proof.

We want to put the integer n on P_n so that P_{n+1} is stationary. There are three distinct cases :

1) We put n between two points A_n and B_n, and we assume A_n, $B_n \neq 0$, and A_n, $B_n \neq n - 1$ (Fig. C1). Since the permutation P_{n+1} thus constructed has to be stationary, one must be able to transform it by adding the point $n + 1$, removing 0, and subtracting 1 to every integer remaining on the circle : one must obtain P_{n+1} again. In other words, the segment of figure C2 must be found on P_{n+1}. Actually, because of the conditions on A_n and B_n, the suppression of the point 0 and the introduction of the point $n + 1$ do not modify the neighbourhood of the point n on P_{n+1}.

The segment of figure C2 being also on P_n (since $A_n - 1 < n - 1$ and $B_n - 1 < n - 1$) it satisfies the rule of the three differences (Prop. 2) ; as a consequence, the segment $A_n - n - B_n$ satisfies it too, and P_{n+1} is angular.
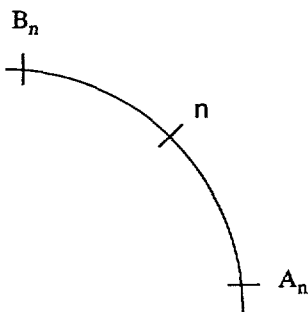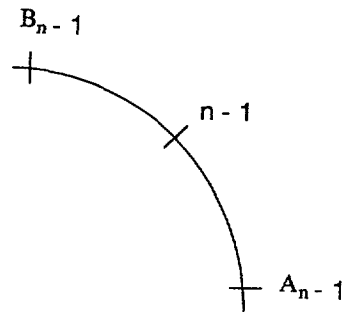

Fig. C1.   Fig. C2.

2) We put n next to $n - 1$ and possibly next to 0 (Fig. C3). Since P_{n+1} has to be stationary, one must find on P_{n+1} the segment of figure C4. This is of course only possible if $A_n = 0$ and $B_n = 1$. Thus we have put n between 0 and $n - 1$, and P_n corresponds to the triple $(n - 1, 1, n)$: we have applied the algorithm of angular descent, therefore P_{n+1} is angular.

3) We put n next to 0 but not next to $n - 1$ (Fig. C5). This time the segment of figure C6 must be found on P_{n+1} and then on P_n. This segment has to satisfy the rule of the three differences, therefore $n = \alpha + \beta$. From this we conclude again that P_{n+1} is angular, since by placing n between 0 and $A_0 = \alpha$ in the permutation $P_n = (\alpha, \beta, n = \alpha + \beta)$ we applied the algorithm of angular descent.
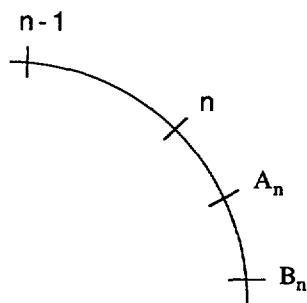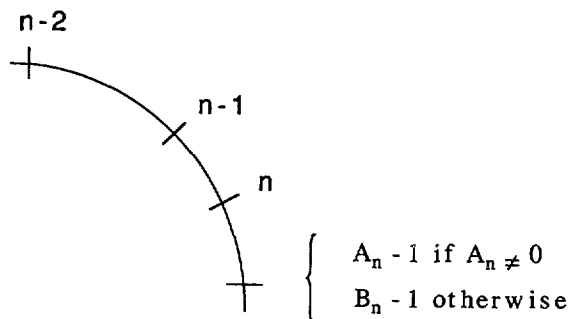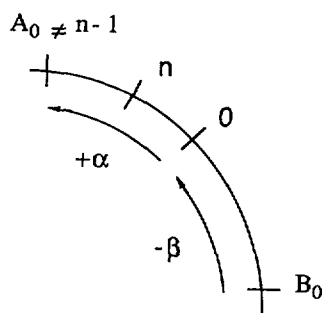
We can now prove :

Fig. C3.

$$\begin{cases} A_n - 1 \text{ if } A_n \neq 0 \\ B_n - 1 \text{ otherwise} \end{cases}$$

Fig. C4.
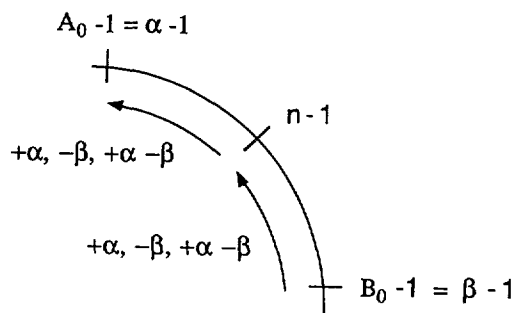

Fig. C5.

Fig. C6.

Proposition 8 (Sect. 4).

A permutation P_n is stationary if and only if it is angular.

Proof.

It is clear that any angular permutation is stationary (consider a realization $T_n(\theta)$ of P_n, construct $P_{n+1} \in D(P_n)$ from $T_{n+1}(\theta)$ and observe that the permutation $P_{n+1}^{(0)}$ is obtained by turning every point of $T_{n+1}(\theta)$ with an angle $- 2 \pi \theta$).

Conversely, as any stationary permutation P_n may be considered as the descent of a stationary permutation P_{n-1} (Lemma C.1), the whole set of stationary permutations is the « stationary descent » of P_3 (with both orientations). But since P_3 is angular, we conclude from Lemma C.2 that any stationary permutation is angular.

Appendix D.

We prove here three lemmas that are obviously equivalent to proposition 9 (Sect. 5.1).

Lemma D.1.

$\forall \Pi_\alpha \in \Omega_q$, Π_α^{-1} *is angular. More precisely,* $\Pi_\alpha^{-1} = \Pi_{p(\alpha)}.$

Proof.

Let us write

$$\Pi_\alpha(i) = C_i \tag{D1}$$

$$C_i + 1 = C_{j(i)} \quad \text{if} \quad C_i = 0, 1, . . , q - 2 \tag{D2}$$

$$C_m = q - 1 . \tag{D3}$$

To show that Π_α^{-1} is angular and belongs to Ω_q, we have to verify that the following differences take only two values (Prop. 2)

$$\Pi_\alpha^{-1}(C_i + 1) - \Pi_\alpha^{-1}(C_i) = j(i) - i \tag{D4}$$

$$\Pi_\alpha^{-1}(0) - \Pi_\alpha^{-1}(q - 1) = -m. \tag{D5}$$

Since Π_α is angular, we know that there exists $k, \ell \in N_q$ such that $0 < k + \ell < q$ and

$$1 = C_{j(i)} - C_i = k\alpha - \ell\beta \tag{D6}$$

where $\beta = q - \alpha$.

We see that any solution k, ℓ of (D6) such that $0 < k + \ell < q$ leads to an unique value of $k + \ell$. In fact, if k', ℓ' also satisfy (D6), then

$$(k - k')\alpha - (\ell - \ell')\beta = 0 \tag{D7}$$

which implies, since $(\alpha, \beta) = 1$, that there exists $c \in Z$ such that

$$k' = k + c\beta \qquad \ell' = \ell + c\alpha \tag{D8}$$

hence $k' + \ell' = k + \ell + cq$ cannot belong to $[0, q]$ if $c \neq 0$.

Now it is clear that

$$\begin{array}{llll} \text{if} & j(i) - i > 0 & \text{then} & j(i) - i = k + \ell \\ \text{if} & j(i) - i < 0 & \text{then} & j(i) - i = k + \ell - q. \end{array} \tag{D9}$$

Let us consider now the value of m. Since Π_α is angular, there exists $k^*, \ell^* \in N_q$ such that $0 < k^* + \ell^* < q$ and they satisfy the equation

$$k^*\alpha - \ell^*\beta = 0 - C_m = 1 - q = 1 - (\alpha + \beta) \tag{D10}$$

i.e.

$$(k^* + 1)\alpha - (\ell^* - 1)\beta = 1 \tag{D11}$$

which implies

$$k^* + 1 + \ell^* - 1 = k^* + \ell^* = k + \ell. \tag{D12}$$

Moreover

$$-m = k^* + \ell^* - q = k + \ell - q. \tag{D13}$$

Thus we have shown that $\Pi_\alpha^{-1} \in \Omega_q$. If we write $\Pi_\alpha^{-1} = \Pi_{\alpha'}$, it follows from the definitions that $\Pi_{\alpha'}(1) = \alpha'$. But we noticed in 3.2.3 that $\Pi_\alpha^{-1}(1) = p(\alpha)$ so that the proof is complete.

Lemma D.2.

$$\forall \Pi_\alpha \in \Omega_q, \qquad \Pi_\alpha(i) = R_q(i\alpha). \tag{D14}$$

Proof.

Let us write as usually $\Pi_\alpha(i) = C_i$. We have seen in 3.2.3 that $\{C_i p/q\} = i/q$ where $p = p(\alpha)$.

In other words

$$\begin{aligned} i &= q\{C_i p/q\} = q(\Pi_\alpha(i)p/q - [\Pi_\alpha(i)p/q]) \\ &= R_q(\Pi_\alpha(i)p) \end{aligned} \tag{D15}$$

or

$$\Pi_\alpha^{-1}(i) = R_q(ip) = \Pi_p(i) \,.$$

Notice that we simply used the identity

$$R_q(i) = i - [i/q] \, q \,. \tag{D16}$$

Conversely

$$\Pi_p^{-1}(i) = \Pi_\alpha(i) = R_q(i\,\alpha) \,. \tag{D17}$$

Lemma D.3.

Ω_q, *provided with the usual composition law of permutations, is a group.*
Proof.

Lemma D.1 shows the existence of an inverse for each element of the group. It is clear that Π_1 corresponds to the identity and belongs to Ω_q.

We still have to prove that

$$\Pi_\alpha \circ \Pi_{\alpha'} \in \Omega_q \qquad \forall \, \Pi_\alpha \,, \Pi_{\alpha'} \in \Omega_q \,. \tag{D18}$$

Now Lemma D.2 shows that

$$\Pi_\alpha \circ \Pi_{\alpha'}(i) = R_q(\alpha R_q(i\,\alpha')) = R_q(iR_q(\alpha\,\alpha')) \,. \tag{D19}$$

Since $(\alpha, q) = 1$ and $(\alpha', q) = 1$, we have $(\alpha\,\alpha', q) = 1$ and then

$$(R_q(\alpha\,\alpha'), q) = 1 \,. \tag{D20}$$

We have therefore proven that

$$\Pi_\alpha \circ \Pi_{\alpha'} = \Pi_{R_q(\alpha\,\alpha')} \in \Omega_q \,. \tag{D21}$$

References

[1] RIVIER N., OCCELLI R., PANTALONI J., LISSOWSKI A., *J. Phys. France* **45** (1984) 49.
[2] LEVITOV L. S., *Phys. Rev. Lett.* **66** (1991) 224 ; *Europhys. Lett.* **14** (1991) 533.
[3] DOUADY S., COUDER Y., *Phys. Rev. Lett.* **68** (1992) 2098.
[4] ADLER I., *J. Theor. Biol.* **45** (1974) 1.
[5] THOMPSON D'ARCY W., On Growth and Form (Cambridge University Press) 2nd edition (1942) p. 912.
[6] COXETER H. S. M., Introduction to Geometry (Wiley and Sons, New York, 1969) p. 160 ; *J. Algebra* **20** (1972) 167.
[7] JEAN R. V., Phytomathématique (Presses de l'Université du Québec, 1978) ; Croissance végétale et morphogenèse (ibid.) ; Mathematical Approach to Pattern and Form in Plant Growth (Wiley and Sons, New York, 1984).
[8] RUTISHAUSER R., *Beitr. Biol. Pflanzen* **57** (1982) 323.
[9] RIVIER N., *J. Phys. Colloq. France* **47** (1986) C3-299.
[10] ROTHEN F., KOCH A. J., *J. Phys. France* **50** (1989) 633 ; *ibid.* **50** (1989) 1603.
[11] SNOW M., SNOW R., *Philos. Trans. Roy. Soc. London Ser. B* **225** (1935) 63.
[12] RICHTER P. H., SCHRANNER R., *Naturwissenschaften* **65** (1978) 319.

[13] SCHOLZ H. J., *Ber. Bunsenges. Phys. Chem.* **89** (1985) 699.

[14] KOCH A. J., GUERREIRO J., BERNASCONI G., SADIK J., to be published.

[15] MARZEC C., KAPPRAFF J., *J. Theor. Biol.* **103** (1983) 201.

[16] MEINHARDT H., Models of Biological Pattern Formation (Academic Press, London, New York, 1982).

[17] TURING A. M., *Philos. Trans. R. Soc. London* **B 237** (1952) 37.

[18] THORNLEY J. H. M., *Ann. Bot.* **39** (1975) 491 ; ibid. 509.

[19] KHINCHIN A. Ya., Continued Fractions (The University of Chicago Press, 1961).

[20] HARDY G. H., WRIGHT E. M., An Introduction to the Theory of Numbers (Clarendon Press) 5th Ed. (Oxford, 1988).

[21] DUNEAU M., KATZ A., *Phys. Rev. Lett.* **54** (1985) 2688.

[22] KATZ A., DUNEAU M., *J. Phys. France* **47** (1986) 181 ; ibid **47-C3** (1986) 103.

[23] KALUGIN P. A., KITAEV A. Yu., LEVITOV L. S., *JETP Lett.* **41** (1985) 145 ; *J. Phys. France Lett.* **46** (1985) L-601.

[24] ELSER V., *Phys. Rev.* **B 32** (1985) 4892.

[25] ELSER V., HENLEY C. V., *Phys. Rev. Lett.* **55** (1985) 2883.

[26] See for instance KLEIN F., Elementary Mathematics from an Advanced Standpoint (McMillan, New York, 1932).

[27] SWIERCZKOWSKI S., *Fundamenta Mathematicae* **46** (1958) 13.

[28] RIVIER N., KOCH A. J., ROTHEN F., in Biologically Inspired Physics, L. Peliti Ed. (Plenum Press, New York and London, 1991).

[29] See the second paper of reference [2].

[30] RIVIER N., *J. Phys. Condens. Matter* **3** (1991) 1.

[31] BOÉCHAT J. (personal communication).

[32] VAN ITERSON G., Mathematische und Mikroskopisch-Anatomische Studien über Blattstellungen (Gustav Fischer, Jena, 1907).