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## Phyllotaxis or the properties of spiral lattices. II. Packing of circles along logarithmic spirals

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**Résumé.** — La phyllotaxie est l'étude des réseaux spiralés qui servent de modèles à de nombreuses structures botaniques (inflorescences de la marguerite, écailles de l'ananas...). Nous en considérons ici une idéalisation géométrique : un réseau de cercles tangents alignés le long d'une spirale logarithmique. Nous fondant sur les conditions de l'empilement compact de tels cercles, nous montrons que les nombres parastichiques doivent appartenir à une suite de Fibonacci généralisée. De plus, si seules des transitions « régulières » de parastichiques se produisent dans le système, la divergence tend vers un nombre noble. C'est au contraire un nombre rationnel qui est atteint au terme d'une suite infinie de transitions singulières.

**Abstract.** — Phyllotaxis can be identified with the study of spiral lattices which are useful as models for many botanical structures (arrangements of the inner florets of a daisy, of the scales of a pineapple...). We consider a geometrical idealization of such networks : a lattice of tangent circles aligned along a logarithmic spiral. using conditions for close-packing of such circles, we show that the parastichy numbers belong to a generalized Fibonacci sequence. Moreover, if « regular » parastichy transitions only occur in the lattice, the divergence tends to a noble number. On the contrary a rational number is reached after an infinite sequence of singular transitions.

### 1. Phyllotaxis, an exotic form of crystallography.

1.1 AN OLD SUBJECT. — The geometry governing the arrangement of some botanical structures is called *phyllotaxis* : it concerns for instance the inner florets of a sunflower or a daisy (spiral phyllotaxis). An other example is cylindrical phyllotaxis which characterizes the arrangement of the scales on a pineapple or on a fir-cone.

In a previous paper [1] hereafter referred to as I, we recall that many mathematicians, physicists and crystallographers have studied phyllotaxis (historical references can be found in I or directly in papers by Adler [2] or Rivier [3] <sup>(1)</sup>). The subject is, however, rather exotic

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<sup>(1)</sup> General references on phyllotaxis are given in I, where we emphasize the difference between conceptions of people from exact sciences (physicists, mathematicians, crystallographers) and those of biologists. A botanist [4], however, has made long ago a work presenting some of the material contained in this paper. An excellent review of geometrical models can be found in Erickson [5]. To our knowledge, the present paper gives nevertheless the first derivation and analysis of the number-theoretical properties involved in the models of spiral lattices.

among physicists. We therefore gave an introduction to it in I. Next section summarizes what is necessary in order to understand the present paper.

**1.2 SPIRAL LATTICES AND PHYLLOTAXIS.** — Consider a logarithmic spiral defined in polar coordinates  $(r, \theta)$  by

$$r = r_0 z^{\theta/(2\pi x)} \tag{1}$$

where  $r_0$ ,  $z$  and  $x$  are three real constants. The *spiral lattice*  $L_s$  is obtained by choosing along this curve a discrete set of points according to

$$r_n = r_0 z^n \quad \theta_n = 2\pi n x \quad n = \dots -1, 0, 1, 2 \dots \tag{2}$$

The curve defined by (1) is generally called *ontogenic spiral*;  $x$  is the *divergence* and  $z$  the *plastochrone ratio*. Their geometrical meaning is immediate. Take two consecutive points of  $L_s$  along the ontogenic spiral, say  $\Pi_n = (r_n, \theta_n)$  and  $\Pi_{n+1} = (r_{n+1}, \theta_{n+1})$ . The divergence  $x$  is linked to the angular distance separating the two considered points :

$$x = \frac{\theta_{n+1} - \theta_n}{2\pi} .$$

On the other hand, the plastochrone ratio  $z$  corresponds to the ratio of their radial distances :

$$z = \frac{r_{n+1}}{r_n} .$$

Figure 1 visualizes these concepts : notice that the eye is not drawn toward the ontogenic

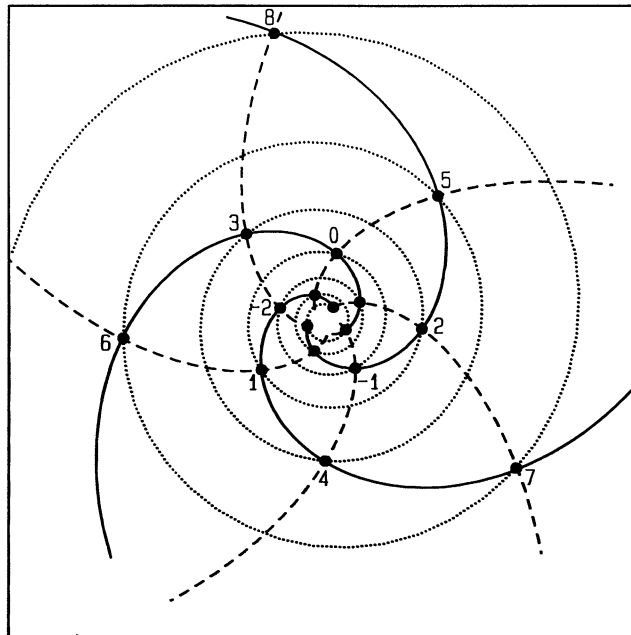


Fig. 1. — The dotted curve is the *ontogenic spiral*  $r = r_0 z^{\theta/(2\pi x)}$ . Filled dots have been placed on the sites of  $L_s$ . Linking neighbouring points of  $L_s$ , one gets the *parastichies* which have been visualized by continuous and dashed lines. The sites of the lattice  $L_s$  have been numbered along the ontogenic spiral, starting from an arbitrary point ; notice how numbers increase regularly along parastichies which, on this figure, belong to the 3- and 5-families (respectively right and left handed).

spiral but rather toward those whorls connecting neighbouring points : these curves are named *parastichies*.

Once the points of the lattice have been numbered along the ontogenic spiral, an obvious fact comes into sight : a given parastichy connects successive points whose indexes always differ by a constant and integer value. For instance, a parastichy could connect points with indexes  $n, n + r, n + 2r \dots$ . The value of  $r$  in this arithmetic sequence characterizes some family of parastichies we naturally call the *r-family* and which is constituted of  $r$  members identified by the different values of  $n = 0, 1, \dots, r - 1$ . As a matter of fact, the distribution of the points of a spiral lattice among the members of a  $r$ -family is isomorphic to the classification of the integers into classes of residues modulo  $r$ .

Since Kepler [2], there is a well-known fact about phyllotaxis : the couple (or triple) of integers  $\{k, \ell\}$  (resp.  $\{k, \ell, m\}$ ) which characterizes the families to which belong the parastichies on a daisy (on a sunflower, ...) are very often successive members of the *Fibonacci sequence*

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

whose members obey the recursion formula

$$f_{n+2} = f_{n+1} + f_n. \tag{3}$$

Less often, the couple  $\{k, \ell\}$  is constituted by two successive members of a generalized Fibonacci sequence  $\{g_n\}$  whose elements still satisfy (3) but with different « initial conditions » ; for instance, the *Lucas sequence* is given by

$$\{g_n\} = 1, 3, 4, 7, 11, 18, 29, 47, 76, 123, \dots$$

The ratio of two successive members of a (generalized) Fibonacci sequence tends to the *golden ratio*  $\tau$  :

$$\lim_{k \rightarrow \infty} \frac{f_{k+1}}{f_k} = \lim_{k \rightarrow \infty} \frac{g_{k+1}}{g_k} = \frac{1 + \sqrt{5}}{2} = \tau$$

(notice that  $\tau = 1 + \tau^{-1}$ ). The development of  $\tau^{-1}$  as a continued fraction is well known <sup>(2)</sup> :

$$\tau^{-1} = \frac{1}{1 + \frac{1}{1 + \frac{1}{1 + \dots}}} \equiv [1, 1, 1, 1, \dots].$$

Hereafter we shall encounter a class of numbers intimately linked to  $\tau$  : *noble numbers*. These are irrationals whose developments as continued fractions allows only a sequence of ones after a definite stage :

$$\begin{aligned} \nu &= \frac{1}{a_1 + \frac{1}{a_2 + \dots \dots + \frac{1}{a_r + \frac{1}{1 + \frac{1}{1 + \dots}}}}} \\ &\equiv [a_1, a_2, \dots, a_r, 1, 1, 1, \dots]. \end{aligned}$$

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<sup>(2)</sup> The notations and properties of continued fractions to be used in this paper are recalled in I. Well-known references on the subject are the books of Khinchin [6], Lang [7] or Perron [8].

As can be noticed, continued fractions will play an essential role in the present paper and especially the notion of *principal convergent*. Let us remember that the  $n^{\text{th}}$  principal convergent  $x_n$  of a number  $x$  in the range  $]0, 1]$  is obtained by truncating its expansion as a continued fraction to the  $n$  first terms :

$$x = [a_1, a_2, \dots, a_n, \dots] \Rightarrow x_n = \frac{p_n}{q_n} = [a_1, a_2, \dots, a_n].$$

The values of  $p_n$  and  $q_n$  may be calculated by use of the recursion formula

$$\left. \begin{aligned} q_0 &= 1 & q_1 &= a_1 & q_{m+2} &= a_{m+2} q_{m+1} + q_m \\ p_0 &= 0 & p_1 &= 1 & p_{m+2} &= a_{m+2} p_{m+1} + p_m \end{aligned} \right\} 0 \leq m. \tag{4}$$

One shows without difficulty that any number  $x = [a_1, \dots, a_n + y]$  with  $0 \leq y < 1$  has the same first  $n$  convergents as  $x_n = [a_1, \dots, a_n]$ .

**1.3 PARASTICHY TRANSITIONS.** — Before going on, let us shortly describe what happens on a daisy (Fig. 2). The size of the florets increases with the distance to the centre of the flower ; we shall see, in section 2, that their growth rate is equal to the plastochrone ratio  $z$  (which corresponds to the rate of increase of the overall pattern). This growth, however, is not exponential, so that if we want to represent a lattice of florets with the help of (2), we have to assume that  $z$  is no longer constant but decreases radially outwards. The value of the

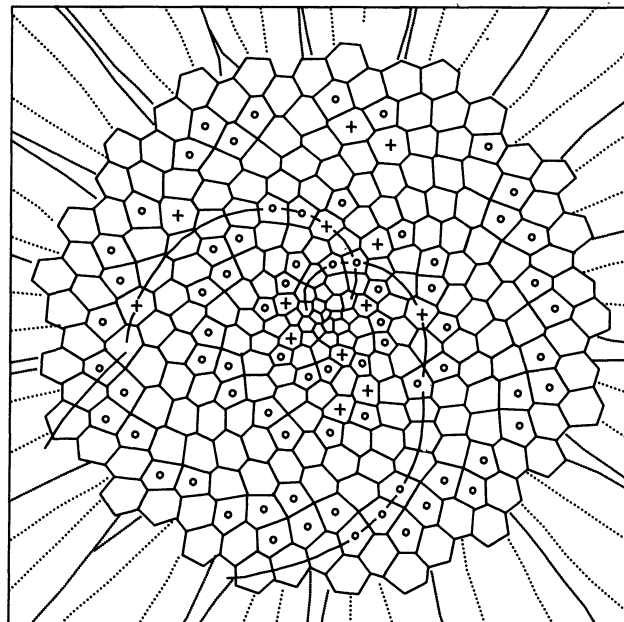


Fig. 2. — A daisy has been pictured. Florets are the units constituting the centre of the flower. They are regularly disposed along parastichies which in this case belong to the 13- and 21-families in the middle part of the flower and to 21- and 34-families in the outer part (some parastichies have been outlined by a full line). Circles of defects are marked, consisting of pentagonal (O) or heptagonal (+) florets ; they act like dislocations allowing the transition between parastichies of the 13-family and those of the 34-family.

divergence  $x$ , on the other hand, seems to be fairly constant throughout the botanical lattice (i.e. the daisy). One clearly distinguishes in the whole arrangement annular zones separated by circles of defects. Within each ring, one finds easily two parastichy families, say  $k_i$  and  $\ell_i$  (where  $i$  indexes the rings from the centre outwards). When one passes from a given region to the outer adjacent one, the  $\{k_i, \ell_i\}$ -families are replaced by the  $\{k_{i+1}, \ell_{i+1}\}$  ones ; the new parastichy numbers are linked to the former ones by

$$k_{i+1} = \ell_i \quad \ell_{i+1} = k_i + \ell_i$$

(one recognizes immediately the similarity of this expression with (3)). It appears that, by going from one ring to the next one, the  $\ell_i$ -family runs continuously across the boundary region, while the  $k_i$ -family disappears, being replaced by the  $\ell_{i+1}$  one. We call this *parastichy transition*.

Transitions are made possible by defects which act like dislocations and which have very interesting properties. We shall not study them here ; let us however mention that structural defects have been described in a very similar case by Rivier *et al.* [9].

In I, we have investigated the modification of the neighbourhood induced by a decrease of the plastochrone ratio  $z$ . We showed that this change is of less importance (being even vanishing if the parastichy numbers  $\{k, \ell\}$  increase) whenever the divergence is a noble number. As the shape of the botanical units (here florets) constituting the lattice is rather stable, it is clear that a divergence preserving the shape of lattice sites is favorable for such arrangements.

A natural question then arises : is there a geometrical mechanism which allows a « noble » divergence to emerge ? In order to give an answer, we shall hereafter construct a geometrical model of phyllotaxis which should be considered as an idealization of botanical structures.

**1.4 PACKING OF CIRCLES ALONG A LOGARITHMIC SPIRAL.** — The model we propose is based on circles packed along a logarithmic spiral. It will fulfill the following requirements :

- A) a circle is centred around each point of  $L_s$  (defined by (2)) ;
- B) each circle is tangent to its four (or six) neighbours ;
- C) there is no overlapping among the circles.

The result to which we shall be lead is pictured in figure 3. Tangent circles align with spirals which can be identified with the parastichies mentioned in section 1.2. The two parastichy numbers  $\{k, \ell\}$  of such spirals are relative prime integers. We shall show that there corresponds a finite range both for the divergence  $x$  and the plastochrone ratio  $z$  which are compatible with the choice of  $\{k, \ell\}$  and the construction of a lattice of circles satisfying conditions A, B, C.

The next section is concerned with the construction of circles tangent along logarithmic spirals. We shall determine the divergences compatible with two given parastichies  $\{k, \ell\}$  along which circles are tangent ; in section 3, parastichy transitions and occurrence of noble numbers will be investigated. We shall show (Sect. 4) that conformal mappings provide a powerful tool to construct similar structures on other surfaces than the plane ; at last, we shall briefly examine what happens if  $k$  and  $\ell$  are no longer required to be relative prime numbers.

## 2. Constructing tangent circles along two families of logarithmic spirals.

Let us consider the spiral lattice  $L_s$  of points  $\Pi_n = (r_n, \theta_n)$ , defined by (2). The divergence  $x$  and the plastochrone ratio  $z$  are arbitrarily fixed. For every value of the index  $n$ , we want to draw a circle  $C_n$  centred on  $\Pi_n$  whose radius  $R_n$  is proportional to the distance

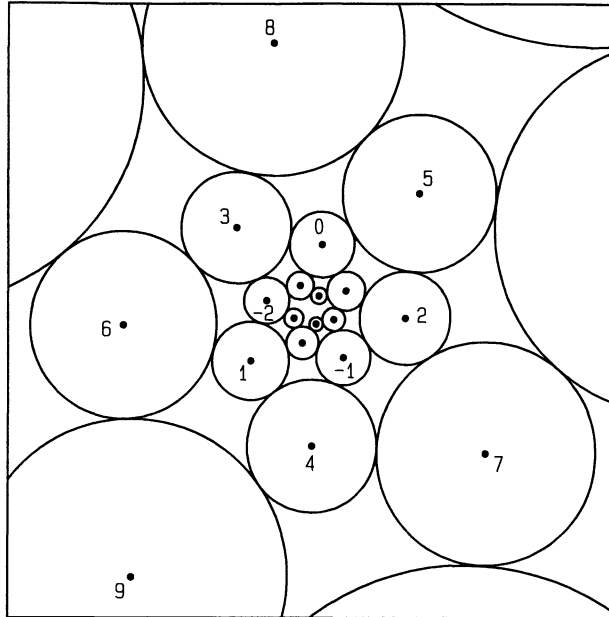


Fig. 3. — A circle is drawn around each site (filled dots) of the spiral lattice  $L_s$ . By suitably choosing their radii, it is possible to get a lattice of tangent circles verifying conditions A, B, C of section 1.4. The lines along which they are in contact are identified with the parastichies.

$r_n$  between  $\Pi_n$  and the origin ( $r = 0$ ) of  $L_s$ . According to (2), we require

$$R_n = R_0 z^n . \tag{5}$$

$R_0$  is still an undetermined length. Our aim is to find a relation between  $x$ ,  $z$ ,  $r_0$  and  $R_0$  in such a way that a given circle  $C_n$  is tangent with  $C_{n+k}$  and  $C_{n+l}$ ,  $k$  and  $l$  being relatively prime integers ( $0 < k < l$ ).

In cartesian coordinates, the vector  $\mathbf{d}_{n,n+m}$  joining the centres  $\Pi_n$  and  $\Pi_{n+m}$  of two circles  $C_n$  and  $C_{n+m}$  writes

$$\mathbf{d}_{n,n+m} = r_0 z^n \begin{pmatrix} z^m \cos \theta_{n+m} - \cos \theta_n \\ z^m \sin \theta_{n+m} - \sin \theta_n \end{pmatrix} .$$

The distance between  $\Pi_n$  and  $\Pi_{n+m}$  is therefore equal to

$$d_{n,n+m} = r_0 z^n \sqrt{z^{2m} - 2 z^m \cos \theta_m + 1} . \tag{6}$$

If we require that circles  $C_n$  and  $C_{n+m}$  of respective radii  $R_n$  and  $R_{n+m}$  are tangent, we have to impose that the distance  $d_{n,n+m}$  between their centres equals the sum of their radii. Using (5) and (6), we get

$$\frac{R_0}{r_0} = \frac{\sqrt{z^{2m} - 2 z^m \cos 2 \pi m x + 1}}{1 + z^m} . \tag{7}$$

As a consequence, the condition of tangency between  $C_n$  and  $C_{n+m}$  depends only on the

difference  $m$  of their ranks along the ontogenic spiral and on  $R_0/r_0$ , the ratio between the radius  $R_0$  of an arbitrary circle of the lattice and the distance  $r_0$  of its centre to the origin. Let us define

$$F_m(x, z) \equiv \frac{\sqrt{z^{2m} - 2z^m \cos 2\pi mx + 1}}{1 + z^m}.$$

If  $x$  is given, the value of  $z$  such that circles  $C_{n+k}$  and  $C_{n+l}$  are both tangent to  $C_n$  is determined by

$$F_k(x, z) = \frac{R_0}{r_0} \quad F_l(x, z) = \frac{R_0}{r_0}. \tag{8}$$

These two equations fix  $R_0/r_0$  and  $z$  as functions of  $x, k$  and  $l$ . The latter parameters are no longer independent if we require that *circles do not overlap* in the lattice. Thus we shall give a link between  $x, k, l$  in order to construct a network satisfying requirements. A, B, C of section 1.4. The following theorem states the conditions under which the construction of a lattice of tangent circles is possible. It states the relation between the parastichy numbers  $k, l$  and the divergence  $x$ .

**Theorem 1.** *Let  $k, l$  be two relatively prime integers,  $0 < k < l$ , and  $x = [a_1, a_2, \dots]$  a real number in the interval  $]0, 1]$ . The construction of a non overlapping lattice of tangent circles is possible for a continuous range of  $x$  if and only if*

$$k = q_r \quad l = q_{r+1} \tag{9}$$

or

$$k = q_r \quad l = q_{r+2} \quad \text{with} \quad a_{r+2} = 1 \tag{10}$$

where  $q_r, q_{r+1}$  and  $q_{r+2}$  are the denominators of three successive principal convergents of  $x$ .

The proof of theorem 1 is outlined in the appendix. Suppose that  $x$  is given ; by use of this theorem, we can find all couples  $\{k, l\}$  allowing the construction of a lattice of tangent circles. Conversely, if  $\{k, l\}$  are given, we may calculate a divergence  $x$  allowing the construction of a non overlapping lattice of circles. We show in appendix that, under the conditions of theorem 1, equations (8) admit two and only two roots  $z_0$  and  $1/z_0$  ; solution  $z_0$  insures the tangency of circle  $C_n$  with  $C_{n+k}$  and  $C_{n+l}$  ; due to the existence of the second solution, namely  $1/z_0$ ,  $C_{n-k}$  and  $C_{n-l}$  are also tangent to  $C_n$ . Notice an important fact : since the condition of tangency does not depend on the index  $n$  (see (7)), the previous statement is true everywhere in the lattice, giving rise to « chains » of tangent circles which are nothing but the parastichies. Due to theorem 1, the divergence  $x$  is of the form (cf. Appendix).

$$x = \frac{p_{r+1} + y p_r}{q_{r+1} + y q_r} = [a_1, \dots, a_r, a_{r+1} + y] \quad \text{if} \quad k = q_r \quad \text{and} \quad l = q_{r+1} \tag{11}$$

or 
$$x = \frac{p_{r+2} + y p_{r+1}}{q_{r+2} + y q_{r+1}} = [a_1, \dots, a_r, a_{r+1}, 1 + y] \quad \text{if} \quad k = q_r \quad \text{and} \quad l = q_{r+2} \tag{12}$$

where  $y$  is a number in the range  $[0, 1[$  and where coefficients  $a_m, p_m$  and  $q_m$  are related by (4).

If  $x$  is given, all couples  $\{k, l\}$  are found by direct application of (4). Conversely, if  $\{k, l\}$  is fixed, one determines  $x = [a_1, a_2, \dots]$  by use of the recurrence relation for  $q_m$ , with the conditions  $k = q_r$  and  $l = q_{r+1}$  (or  $k = q_r, l = q_{r+2}$  and  $a_{r+2} = 1$ ).



### 3. Transitions between close-packed lattices.

**3.1 REGULAR AND SINGULAR TRANSITIONS.** — The previous construction insures that, for any  $n$ ,  $C_{n+k}$  and  $C_{n+l}$  are tangent to  $C_n$ . However, the relative position of circles  $C_n$  and  $C_{n+k+l}$  is still free and they can become tangent. In the latter case,  $C_n$  is in contact with six neighbouring circles : this is what we call *close-packing of circles*. It happens that a parastichy transition occurs each time close-packing is realized. Conditions under which this is possible are given by theorem 2.

**Theorem 2.** *Close packing of circles occurs in  $L_s$  if and only if*

$$k = q_r \quad \ell = q_{r+1} \quad k + \ell = q_{r+2} \quad (13)$$

where  $q_r$ ,  $q_{r+1}$  and  $q_{r+2}$  are the denominators of three successive principal convergents of the divergence  $x$ . If close-packing takes place in the lattice, the values of the plastochrone ratio  $z$  and of the divergence  $x$  are completely and uniquely defined by  $k$  and  $\ell$ .

The proof is sketched in appendix. As an immediate consequence of (4) and (13), the  $(r+2)^{\text{th}}$  coefficient of the development of  $x$  as a continued fraction has to be equal to one :  $a_{r+2} = 1$ .

Starting from a situation where the parastichy numbers are  $\{k, \ell\}$ , a progressive reduction of the plastochrone ratio  $z$  leads to a situation of close-packing where three parastichy families, namely  $\{k, \ell, k + \ell\}$ , are visible. A slight decrease of  $z$  induces a transition : one of the former families, either  $k$  or  $\ell$ , has to disappear (the process is illustrated in Fig. 4). There

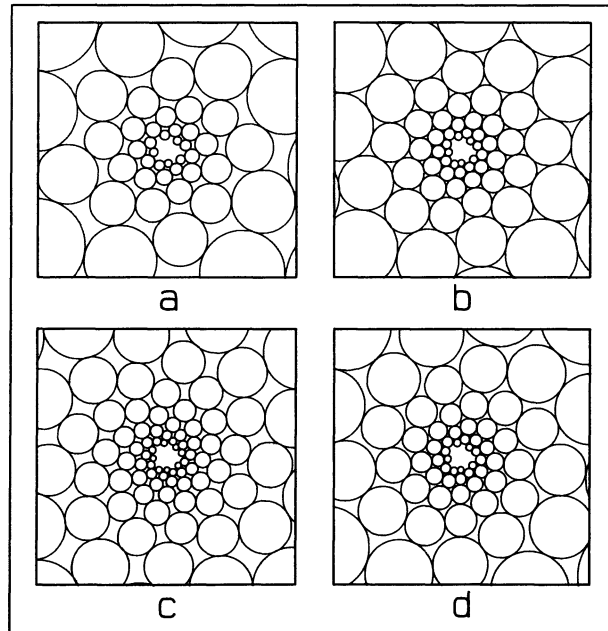


Fig. 4. — Starting from a given configuration (a) with parastichy number  $\{k, \ell\}$  (here  $k = 5$ ,  $\ell = 8$ ), the plastochrone ratio  $z$  is slowly reduced. The lattice becomes more and more compact, up to close-packing (b) where the three parastichy families  $\{k, \ell, k + \ell\} = \{5, 8, 13\}$  are apparent. Further decrease of  $z$  leads to a transition which is either regular (c) with parastichy numbers  $\{\ell, k + \ell\} = \{8, 13\}$  or singular (d) where the couple of parastichy numbers is  $\{k, k + \ell\} = \{5, 13\}$ .

is a kind of « bifurcation » where the system can proceed along two different ways : if the  $k$ -family vanishes (Fig. 4c), we have a transition

$$\{k, \ell\} \rightarrow \{\ell, k + \ell\}$$

which we shall hereafter call *regular transition*, in opposition to the case where the  $l$ -family disappears (Fig. 4d)

$$\{k, \ell\} \rightarrow \{k, k + \ell\}$$

which is called *singular*.

A regular transition is characterized by the fact that the couple of parastichies  $\{q_r, q_{r+1}\} = \{k, \ell\}$  is replaced by the couple  $\{q_{r+1}, q_{r+2}\} = \{\ell, k + \ell\}$  (so that  $a_{r+2} = 1$ ). According to (11), the divergence, up to the transition, is equal to

$$x_{k, \ell}(y) = \frac{p_{r+1} + yp_r}{q_{r+1} + yq_r} = \frac{p_{r+1} + yp_r}{\ell + yk}$$

and is defined for  $0 \leq y < 1$ ;  $x_{k, \ell}(y)$  is compatible with the choice of  $C_{n+k}$  and  $C_{n+\ell}$  as circles tangent to  $C_n$  (overlapping of  $C_n$  and  $C_{n+\ell-k}$  (or  $C_{n+\ell+k}$ ) can and does occur for  $y$  close to 0 or 1). For some  $y_c$ , there is simultaneous tangency of  $C_n$  with  $C_{n+k}$ ,  $C_{n+\ell}$  and  $C_{n+k+\ell}$ . The corresponding value of the divergence  $x_{k, \ell}(y_c)$  must then be equal to a divergence  $x_{\ell, k+\ell}(y_c^R)$  for which  $C_{n+\ell}$  and  $C_{n+k+\ell}$  are tangent to  $C_n$ ; the value of  $y_c^R$  must be such that

$$x_{k, \ell}(y_c) = \frac{p_{r+1} + y_c p_r}{\ell + y_c k} = \frac{p_{r+2} + y_c^R p_{r+1}}{(k + \ell) + y_c^R \ell} = x_{\ell, k+\ell}(y_c^R)$$

which yields

$$y_c^R = \frac{1}{y_c} - 1.$$

This shows that  $y_c$  belongs to the interval  $\left] \frac{1}{2}, 1 \right[$  (since  $0 \leq y_c^R < 1$ ). Notice that a regular transition (RT) allows us to fix one more term in the development of the divergence  $x$  as a continued fraction :

$$x_{k, \ell}(y) = [a_1, \dots, a_{r+1} + y] \xrightarrow{\text{RT}} x_{\ell, k+\ell}(y') = [a_1, \dots, a_{r+1}, 1 + y'].$$

In the case of a singular transition (ST) the situation is different. To analyse the transition in the same way, we ought to claim that the transition is characterized by the substitution of the couple  $\{k, \ell\}$  by  $\{k, k + \ell\}$ . If we apply the algorithm (4), there is no difficulty in finding the sequence of  $a_m$  corresponding to the new set of parastichies ; we get

$$x_{k, \ell}(y) = [a_1, \dots, a_{r+1} + y] \xrightarrow{\text{ST}} x_{k, k+\ell}(y'') = [a_1, \dots, a_{r+1} + 1 + y''], \tag{14}$$

so that the number of known coefficients  $a_m$  is the *same* before and after a singular transition. There is another important difference with respect to the case of a regular transition ; when circles  $C_{n+k}$ ,  $C_{n+\ell}$  and  $C_{n+k+\ell}$  are simultaneously tangent to  $C_n$ , (14) shows that  $y_c^S$  satisfying

$$x_{k, \ell}(y_c) = x_{k, k+\ell}(y_c^S)$$

is given by

$$y_c^S = y_c - 1 < 0 .$$

This means that our artificial substitution of  $\{k, \ell\}$  by  $\{k, k + \ell\}$  as two successive denominators of the principal convergents of order  $r$  and  $r + 1$  is not allowed since  $y_c^S$  should be positive. Figure 4d shows the geometrical expression of this oddity : the 5- and 13-parastichies have the same chiralities which clearly shows that 5 and 13 cannot correspond to denominators of two successive principal neighbours of the divergence (in which case the chiralities should be opposite [1]). As a matter of fact,  $k$  and  $\ell$  correspond to bisuccessive convergents of the divergence, as stated by (10).

However, the difficulty just mentioned is not a serious one. If we go away from the transition point by modifying the divergence  $x$  and keeping both circles  $C_{n+k}$  and  $C_{n+k+\ell}$  tangent to  $C_n$ , the situation gradually changes :  $y''$  increases and soon gets positive, showing that  $C_{n+k+\ell}$  revolved around  $C_n$  and crossed the axis going through the centre of  $C_n$  and the origin of  $L_s$  : now  $k$  and  $k + \ell$  actually correspond to denominators of successive principal convergents of the divergence  $x$ .

**3.2 CASCADE OF BIFURCATIONS.** — We are now able to get a general picture of the process occurring when  $z$  is reduced (Fig. 5). Let us start from an arbitrary couple  $\{k, \ell\}$  of relatively prime integers. We can determine the values of  $x$  and  $z$  corresponding to the divergence and plastochrone ratio of a spiral lattice of circles such that  $C_{n+k}$  and  $C_{n+\ell}$  are both tangent to  $C_n$  for any integer  $n$ . Moreover, we can always choose  $(x, z)$  so that there is no overlapping in the lattice : this corresponds to a point of the diagram  $z - x$  in figure 5. For instance, the curve  $\{2, 3\}$  gives the set of points  $(x, z)$  compatible with the choice  $k = 2, \ell = 3$ . If we reduce  $z$ , we follow this curve until we reach a bifurcation which corresponds to the simultaneous tangency of  $C_{n+2}, C_{n+3}$  and  $C_{n+5}$  with  $C_n$ . At this stage, we have the choice to follow either curve  $\{2, 5\}$  or  $\{3, 5\}$  ; in both cases we shall reach again and again new bifurcations. If we reduce  $z$  to the limit value  $z_L = 1$ , we shall overstep an infinite sequence of bifurcations.

Figure 5 illustrates some general properties which can be deduced from the material enclosed in the previous sections :

- after a regular transition RT, the sense of variation of the divergence  $x$  always changes. Moreover, a RT adds a new step in the fixed part of the development of the divergence as a continued fraction :

$$[a_1, \dots, a_{r+1} + y] \xrightarrow{\text{RT}} [a_1, \dots, a_{r+1}, 1 + y'] \quad (0 \leq y, y' < 1) ;$$

- after a singular transition ST, the sense of variation of the divergence does not change. A ST never adds a step to the fixed part of the development of the divergence :

$$[a_1, \dots, a_{r+1} + y] \xrightarrow{\text{ST}} [a_1, \dots, a_{r+1} + 1 + y''] \quad (0 \leq y, y'' < 1) .$$

As a consequence, an infinite sequence of regular transitions necessarily leads to a noble number as the limit divergence :

$$[a_1, \dots, a_{r+1} + y] \xrightarrow{\text{cascade of RT}} [a_1, \dots, a_{r+1}, 1, 1, \dots] = [a_1, \dots, a_{r+1} + \tau^{-1}] = x_{k, \ell}(\tau^{-1}) .$$

Between two regular transitions, the divergence always crosses the limiting noble divergence : it oscillates closer and closer to  $x_{k, \ell}(\tau^{-1})$ .

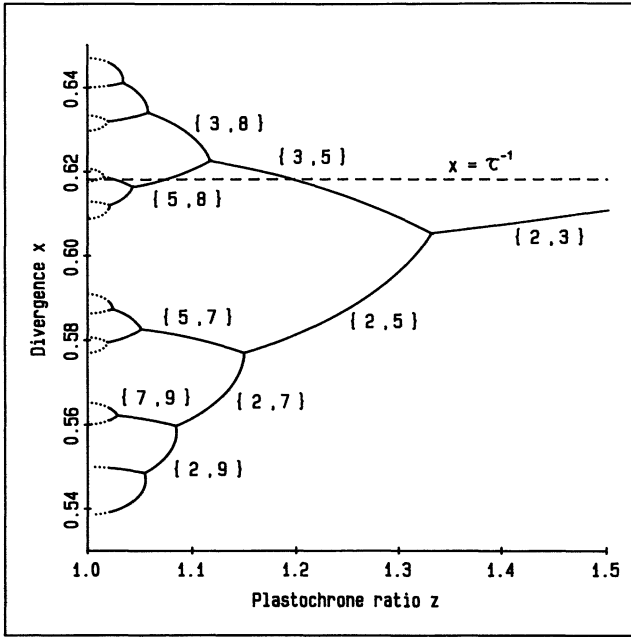


Fig. 5. — The curves mark the value of  $x$  and  $z$  for which the construction of a lattice of tangent circles is possible. Starting with a system characterized by parastichy numbers  $\{k, \ell\}$  (here  $\{2, 3\}$ ), a reduction of  $z$  leads to close-packing of circles. A further decrease of  $z$  may then produce two different situations : either the  $k$ -parastichies disappear (*regular transition*  $\{k, \ell\} \rightarrow \{\ell, k + \ell\}$ ), or the  $\ell$ -parastichies vanish (*singular transition*  $\{k, \ell\} \rightarrow \{k, k + \ell\}$ ). In both cases, further reduction of  $z$  leads to new transitions.

On the other hand, an infinite sequence of singular transitions leads to a rational limit

$$[a_1, \dots, a_{r+1} + y] \xrightarrow{\text{cascade of ST}} \lim_{j \rightarrow \infty} [a_1, \dots, a_r, a_{r+1} + j] = [a_1, \dots, a_r].$$

Each real number  $0 < x \leq 1$  can be reached through a cascade of transitions (one can show that the way a number is reached is unique if it is irrational ; on the other hand, there exist two different paths if the number is rational). For instance, the cascade of transitions leading to the number  $x = [a_1, a_2, \dots]$  is obtained through the following recipe.

- Choose an arbitrary value for  $r$ .
- Calculate the values of both rational fractions  $[a_1, \dots, a_r] = p_r/q_r$  and  $[a_1, \dots, a_{r+1}] = p_{r+1}/q_{r+1}$ .
- Call  $k = q_r$  and  $\ell = q_{r+1}$  ; choose a couple  $(x, z)$  along the segment  $\{k, \ell\}$  of the diagram  $z - x$ .
- Let the point  $(x, z)$  follow the curve  $\{k, \ell\}$  in the direction of decreasing  $z$  ;  $(x, z)$  undergoes a cascade of bifurcations according to the code

$$\underbrace{R, S, S, \dots, S}_{a_{r+2} \text{ transitions}}, \underbrace{R, S, S, \dots, S}_{a_{r+3} \text{ transitions}}, \underbrace{R, S, S, \dots, S}_{a_{r+4} \text{ transitions}}, \dots$$

where R(S) symbolizes a regular (singular) transition.

Let us come back to phyllotaxis ; there is no reason to assume that the probabilities of either transitions are equal among plants. There are at least two arguments which strongly favour regular transitions :

- As discussed above, a spiral lattice undergoing a regular transition jumps from  $(x_{k, \ell}(\tau^{-1}), z_1)$  to  $(x_{\ell, k+\ell}(\tau^{-1}), z_2)$  with  $z_1 > z_2$  and  $x_{k, \ell}(\tau^{-1}) = x_{\ell, k+\ell}(\tau^{-1})$ . Such a jump can be considered as a finite transition. In I, we called it *standard transition* and showed that it is characterized by the fact that the Voronoi polygon around each point of the lattice  $L_s$  changes the less ; we used this argument of shape invariance to favour phyllotaxis with noble divergences (a singular transition cannot lead to a standard transition !). Thus shape invariance of the environment of a circle (corresponding to a floret or a scale in a plant) favours regular transitions.

- A cascade of regular transitions leads to oscillations of the divergence  $x$  with ever decreasing amplitude. On the other hand, a cascade of singular transitions leads to a steadily increasing (or decreasing) divergence. Thus regular transitions need less important rearrangement of the structure than singular ones.

In the theory of approximation of irrational numbers by rational fractions, noble numbers (and among them the golden section  $\tau$ ) are in some respect the « opposite » of rational numbers because they are most slowly approximated by rational numbers. We find here an analogous property in phyllotaxis : noble and rational divergences result from « opposite » cascades of merely regular or singular transitions. On the other hand, any other real number corresponds to an intermediate case as the result of a cascade of both types of transitions. For instance, quadratic algebraic divergences result from a cascade characterized by a periodic sequence of regular and singular transitions.

This discussion may seem of little interest for the phyllotaxis or related physical systems. However, models of packing of growing discs [10] show important differences in the stability of the system according to the parameters involved. We shall discuss in a future paper [11] how their stability is related to the algebraic character of the limit divergence.

**4. Conformal applications.**

Up to here, we have been concerned only with plane phyllotaxis. One may ask whether it is possible to reproduce the same results (lattice of tangent circles, parastichy transitions...) on other surfaces like spheres, cones, cylinders...

The transposition to the sphere is immediate : the *stereographic projection* which maps the sphere on the plane is the ideal tool since it is a circle preserving transformation (Fig. 6b).

Let us now shortly describe the method to construct lattices of tangent circles on a cone (Fig. 6c). The transformation

$$u + iv = r e^{i\theta \sin \frac{\psi}{2}}$$

maps the strip  $-\pi \leq \theta < \pi$  on an angular region

$$-\pi \sin \frac{\psi}{2} \leq \arg (u + iv) < \pi \sin \frac{\psi}{2}$$

which can be thought of as a cone with apex angle  $\psi$  unwrapped on the plane. By use of this transformation, any point  $(r_n, \theta_n)$  of the plane lattice  $L_s$  is mapped on a point  $(u_n, v_n)$  of the cone. The condition of tangency of circles  $C_n$  and  $C_{n+m}$  on a cone, is then readily found to be

$$\frac{R_0}{r_0} = \frac{\sqrt{z^{2m} - 2 z^m \cos \left( 2\pi m x \sin \frac{\psi}{2} \right) + 1}}{1 + z^m}$$

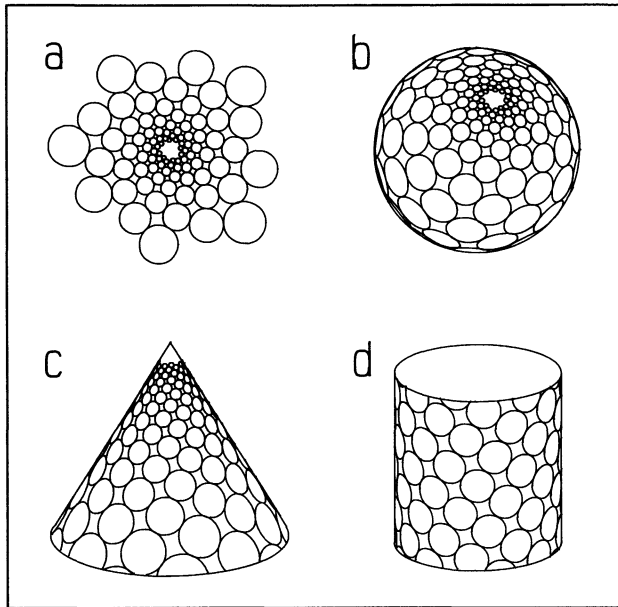


Fig. 6. — By use of conformal transformations, one easily gets lattices of tangent circles on other surfaces than the plane (a), here a sphere (b), a cone (c) and a cylinder (d).

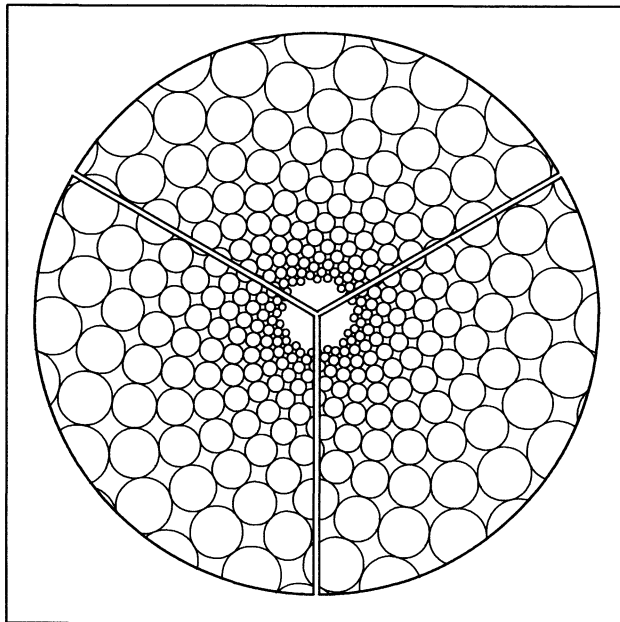


Fig. 7. — A  $\{k, \ell\}$  phyllotaxis has been drawn on a cone with apex angle equal to  $2 \arcsin(1/m)$ . Unrolling  $m$  times this cone on a plane produces a phyllotaxis characterized by parastichy numbers  $\{k', \ell'\} = \{mk, m\ell\}$ . On this picture,  $m = 3$  and  $\{k, \ell\} = \{5, 8\}$ .

This equation generalizes (7). One notices immediately that it contains the plane phyllotaxis (Fig. 6a) as well as phyllotaxis on a cylinder (Fig. 6d) as limiting cases when  $\psi \rightarrow \pi$  or  $\psi \rightarrow 0$  respectively. Moreover, the construction on a cone provides the key to the following question : is it possible to find spiral networks without the restriction that  $k$  and  $\ell$  are relatively primes ?

Let us take  $\{k', \ell'\}$ , two such numbers. One writes  $k' = mk$  and  $\ell' = m\ell$ ,  $m$  being the greatest common divisor of  $k'$  and  $\ell'$ . One can then draw a lattice of tangent circles characterized by the parastichy numbers  $\{k, \ell\}$  on a cone with apex angle  $\psi = 2 \arcsin (1/m)$ . Unrolling this cone  $m$  times on the plane gives rise to a phyllotaxis with circles tangent along  $k'$ - and  $\ell'$ -parastichies (Fig. 7). Such structures are often encountered in phyllotaxis and are called *decussate* if  $m = 2$ , *tricussate* if  $m = 3$ , ... ( $m$  corresponds to the *jugacy* introduced by Turing [5]).

Many other mappings produce funny results which are, however, of little use in phyllotaxis. Let us mention that one obtains a generalization of Coxeter's *loxodromic sequences of tangent circles* by inversion of  $L_s$  in an arbitrary circle [12].

## 5. Conclusions.

The results of this paper are of purely geometrical nature. They complement the conclusions drawn from I. It has been shown that a phyllotactic pattern constructed along a logarithmic spiral has peculiar properties, related to the reduction of the plastochrone ratio  $z$ . If we decrease  $z$ , a parastichy transition eventually occurs. In I, we have shown that the transitions which happen in a lattice with noble divergences  $x = [a_1, a_2, \dots, a_r, 1, 1, 1, \dots]$  are characterized by a peculiar symmetry : local shape invariance is best preserved in this case. In the present paper, we have reached the same conclusions by studying a geometrical idealization of phyllotaxis.

The latter values of the divergence are precisely those for which the two parastichy numbers correspond to successive numbers of any sequence obeying the recursion formula

$$f_{k+2} = f_{k+1} + f_k.$$

Actually, most plants precisely belong to this category. Now arguments using such simple concepts as « non-overlapping circles » and « shape invariance of the pattern » are certainly required in order to understand the meaning of the occurrence of phyllotactic networks. For instance, usual crystallography makes an extensive use of similar concepts such as compact stacking of spheres or invariance through some space transformation.

However, using and recognizing some symmetries or geometrical properties is not equivalent to bringing forward a precise mechanism. In this work, we have tried to show that if the plastochrone ratio, identified with the growth rate of the unit cells, decreases radially outwards, parastichy transitions have to appear. Coupled with some geometrical constraint analogous to the absence of circle-overlapping, this occurrence of transitions leads to noble divergences.

## Acknowledgments.

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## Appendix.

Let us precise the notations and concepts which will be used throughout the present appendix. References to paper I will be made in the form (I .  $j$ ), where  $j$  points to the numbering of the formulas therein. We shall consider a real number  $x$  (to be identified with the divergence) in the interval  $]0, 1[$  and its development as a continued fraction

$$x = [a_1, a_2, \dots].$$

The  $r^{\text{th}}$  principal convergent of  $x$  is given by

$$x_r = [a_1, \dots, a_r] = \frac{p_r}{q_r}$$

and the intermediate convergents (if they exist) are

$$x_{r,j} = \frac{j p_{r+1} + p_r}{j q_{r+1} + q_r} = \frac{p_{r,j}}{q_{r,j}} \quad 0 < j < a_{r+2}.$$

We shall consider two relatively prime and positive integers  $k$  and  $\ell$  verifying

$$0 < k < \ell.$$

A lattice of circles such that circles  $C_{n+k}$  and  $C_{n+\ell}$  are both tangent to  $C_n$  for any integer  $n$  has to verify (8) or, more explicitly

$$F_k^2(x, z) = F_\ell^2(x, z) \tag{15}$$

where

$$F_m^2(x, z) = \frac{z^{2m} - 2z^m \cos 2\pi mx + 1}{(1 + z^m)^2} = 1 - \left( \frac{\cos \pi mx}{\cosh \left( \frac{m}{2} \ln z \right)} \right)^2. \tag{16}$$

The condition of non overlapping expresses the fact that, for two arbitrary circles  $C_n$  and  $C_{n+m}$ , the distance separating their centres has to be greater than or equal to the sum of their radii. This, if  $C_{n+k}$  and  $C_n$  are tangent, is equivalent to

$$F_m^2(x, z) \geq F_k^2(x, z) \quad \text{for all } m \neq 0. \tag{17}$$

We shall successively show under which conditions equation (15) admits positive real solutions  $z$ , how many such solutions exist and how  $k, \ell, x$  have to be related in order to satisfy (17).

**Proposition 1.** *Equation (15) admits solutions if and only if  $\cos^2 \pi kx \leq \cos^2 \pi \ell x$ . If this is verified, there exist two and only two positive real solutions  $z_0$  and  $1/z_0$ .*

*Proof.* By use of (16), equation (15) rewrites

$$\frac{\cos^2 \pi \ell x}{\cos^2 \pi kx} = \frac{\cosh^2 \left( \frac{\ell}{2} \ln z \right)}{\cosh^2 \left( \frac{k}{2} \ln z \right)}. \tag{18}$$

Suppose  $x$  fixed. Since  $k < \ell$ , the right hand side of this relation is, for  $z \geq 1$ , an increasing function of  $z$ , its lower bound being equal to 1. It is then clear that (18) admits a solution  $z_0$  if and only if  $\cos^2 \pi kx \leq \cos^2 \pi \ell x$  and that this solution is unique in the interval  $1 \leq z < \infty$ . By symmetry, if  $z_0$  is a solution of (18), so is  $1/z_0$ . This completes the proof.

**Proposition 2.** *The construction of a non overlapping lattice of tangent circles is possible only if  $k$  and  $\ell$  are denominators of two principal convergents of  $x$ .*

*Proof.* We shall show that if  $k$  and  $\ell$  are not related to principal convergents of  $x$ , condition (17) cannot be satisfied for any value of  $m$ . Let us first suppose that  $k$  (or  $\ell$ ) is equal to the



denominator  $q_{r,j}$  of an intermediate convergent of  $x$ . Due to properties (I.20) and (I.21), one has

$$|q_{r+1}x - p_{r+1}| \leq |q_{r,j}x - p_{r,j}| \leq \frac{1}{2}$$

which induces

$$\cos^2 \pi q_{r,j} x \leq \cos^2 \pi q_{r+1} x .$$

Since  $q_{r+1} < q_{r,j}$ , the following relation holds

$$\frac{\cos^2 \pi q_{r,j} x}{\cosh^2 \left( \frac{q_{r,j}}{2} \ln z \right)} < \frac{\cos^2 \pi q_{r+1} x}{\cosh^2 \left( \frac{q_{r+1}}{2} \ln z \right)} .$$

This last inequality, introduced in (17), expresses that, if  $k$  (or  $\ell$ ) is related to an intermediate convergent of the divergence  $x$ , the lattice presents necessarily overlapping among the circles since  $F_{q_{r+1}}^2(x, z) < F_{q_{r,j}}^2(x, z)$ .

Suppose now that  $k$  (or  $\ell$ ) is neither related to a principal nor to an intermediate convergent of  $x$ ; let  $q_r$  be the greatest denominator of a principal convergent of  $x$  verifying  $q_r < k$  and let  $p$  be the nearest integer to  $kx$ . The following inequality holds (see (I.21)) :

$$|q_r x - p_r| \leq |kx - p| .$$

This leads to

$$\frac{\cos^2 \pi kx}{\cosh^2 \left( \frac{k}{2} \ln z \right)} < \frac{\cos^2 \pi q_r x}{\cosh^2 \left( \frac{q_r}{2} \ln z \right)} .$$

Again, (17) is not verified : circles  $C_{n+q_r}$  and  $C_n$  overlap for any  $n$ .

As a conclusion, if  $k$  and  $\ell$  are not both equal to denominators of principal convergents of  $x$ , overlapping occurs in the lattice.

**Proposition 3.** *A non overlapping lattice of tangent circles can always be constructed if  $\{k, \ell\} = \{q_r, q_{r+1}\}$  or if  $\{k, \ell\} = \{q_r, q_{r+2}\}$  and  $a_{r+2} = 1$ .*

*Outline of the proof.* We shall consider successively the three cases  $\{k, \ell\} = \{q_r, q_{r+1}\}$  with  $\ell < 2k$ ,  $\{k, \ell\} = \{q_r, q_{r+1}\}$  with  $\ell > 2k$  and  $\{k, \ell\} = \{q_r, q_{r+2}\}$ .

a)  $\{k, \ell\} = \{q_r, q_{r+1}\}$  with  $\ell < 2k$ .

The divergence is equal to (see (I.15))

$$x(y) = \frac{p_{r+1} + y p_r}{q_{r+1} + y q_r} \quad 0 \leq y < 1 .$$

Let us take  $y = \tau^{-1}$  and suppose that (15) is verified. One calculates without difficulty that, for  $j \geq 1$ , one has [7]

$$|q_{r+j}x - p_{r+j}| = \frac{1}{\tau} |q_{r+j-1}x - p_{r+j-1}| = \frac{\tau^{1-j}}{\tau q_{n+1} + q_n} . \tag{19}$$

We shall prove that

$$\begin{aligned} \frac{\cos^2 \pi q_{r+j+1} x}{\cosh^2 \left( \frac{q_{r+j+1}}{2} \ln z \right)} &\leq \frac{\cos^2 \pi q_{r+j} x}{\cosh^2 \left( \frac{q_{r+j}}{2} \ln z \right)} \Rightarrow \\ &\Rightarrow \frac{\cos^2 \pi q_{r+j+2} x}{\cosh^2 \left( \frac{q_{r+j+2}}{2} \ln z \right)} < \frac{\cos^2 \pi q_{r+j+1} x}{\cosh^2 \left( \frac{q_{r+j+1}}{2} \ln z \right)} \quad \text{for all } j \geq 0. \end{aligned}$$

Due to (19), one can take benefit of the concavity of  $\cos \alpha$  ( $0 \leq \alpha \leq \pi/2$ ) and of the convexity of  $\cosh \beta$  in order to write

$$\begin{aligned} \frac{\cos^2 \pi q_{r+j+2} x}{\cosh^2 \left( \frac{q_{r+j+2}}{2} \ln z \right)} &\leq \frac{2 \cos^2 \pi q_{r+j+1} x - \cos^2 \pi q_{r+j} x}{\cosh^2 \left( \frac{q_{r+j+2}}{2} \ln z \right)} \leq \frac{\cos^2 \pi q_{r+j+1} x}{\cosh^2 \left( \frac{q_{r+j+1}}{2} \ln z \right)} \times \\ &\times \frac{2 \cosh^2 \left( \frac{q_{r+j+1}}{2} \ln z \right) - \cosh^2 \left( \frac{q_{r+j}}{2} \ln z \right)}{\cosh^2 \left( \frac{q_{r+j+2}}{2} \ln z \right)} < \frac{\cos^2 \pi q_{r+j+1} x}{\cosh^2 \left( \frac{q_{r+j+1}}{2} \ln z \right)}. \end{aligned}$$

So that (17) is true for any  $m = q_{r+j}$ ,  $j \geq 0$ . The proof is immediately extended to any integer  $m > q_r$  (the demonstration uses the same tools as the one of proposition 2). The self-similarity of the lattice  $L_s$  [1] allows to conclude that, if no overlapping occurs for  $m > q_r$ , the same remains true for  $m < q_r$ .

b)  $\{k, \ell\} = \{q_r, q_{r+1}\}$  and  $\ell > 2k$ .

The divergence writes

$$x(y) = \frac{p_{r+1} + yp_r}{q_{r+1} + yq_r} \quad 0 \leq y < 1.$$

We shall prove that  $y = 0$  leads to a non overlapping lattice of tangent circles. The divergence  $x(0)$  is rational and its last convergent is  $p_{r+1}/q_{r+1}$ . Since  $\ell > 2k$ ,  $a_{r+1}$  is greater than one ; this means that there are intermediate convergents between  $p_r/q_r$  and  $p_{r+1}/q_{r+1}$  whose denominators are determined by

$$q_{r-1,j} = jq_r + q_{r-1} \quad 0 < j < a_{r+1}.$$

and which verify

$$|q_r x - p_r| \leq |q_{r-1,j} x - p_{r-1,j}| \leq \frac{1}{2}$$

so that the following inequality is true :

$$\frac{\cos^2 \pi q_{r-1,j} x}{\cosh^2 \left( \frac{q_{r-1,j}}{2} \ln z \right)} < \frac{\cos^2 \pi q_r x}{\cosh^2 \left( \frac{q_r}{2} \ln z \right)}.$$

Introducing this in (17), one finds that circles  $C_{n+q_{r-1,j}}$  and  $C_n$  do not overlap. The proof is immediately extended to any integer  $m$  (see case (a)).

c)  $\{k, \ell\} = \{q_r, q_{r+2}\}$

We shall admit without demonstration that  $a_{r+2}$  has to be equal to one in order to avoid overlapping : there are no real difficulties to prove it, but the demonstration is too long to be given here. The divergence is, in this last case, given by

$$x(y) = \frac{p_{r+2} + y p_{r+1}}{q_{r+2} + y q_{r+1}}$$

The choice  $y = 0$  leads to a non overlapping lattice as we shall show hereafter. Let us first prove that  $C_{n+q_{r+1}}$  and  $C_n$  are not in contact, by direct computation, one finds that

$$\cos^2 \pi q_r x = \cos^2 \pi q_{r+1} x,$$

so that (17) is verified for  $m = q_{r+1}$ . Now  $x(0)$  is rational, its last convergent being  $p_{r+2}/q_{r+2}$ . The remaining of the proof can be copied on case (b).

This completes the « demonstration » of proposition 3.

**Proposition 4.** *A non overlapping lattice of tangent circles cannot be constructed if  $\{k, \ell\} = \{q_r, q_{r+v}\}$  with  $v > 2$ .*

*Outline of the proof.* A demonstration of this statement being rather long, we shall only outline an intuitive argument in order to make the proposition plausible from a geometrical point of view.

Consider two adjacent parastichies belonging to the  $k$ -family. The first one is composed with circles  $C_{n+jk}$  ( $j = \dots, -1, 0, 1, \dots$ ) ; circles  $C_{n+\ell+jk}$  ( $j = \dots, -1, 0, 1, \dots$ ) form the second one (by *adjacent*, we mean that  $C_{n+jk}$  and  $C_{n+\ell+jk}$  are tangent for any  $j$ ). Due to (4), one can always write

$$\ell = q_{r+v} = t q_{r+1} + s q_r = t q_{r+1} + s k$$

where  $s$  and  $t$  are two integers,  $t$  being greater than 1. This means that  $C_{n+\ell-sk}$  and  $C_n$  (which are lying on two adjacent  $k$ -parastichies) are located on the same  $q_{r+1}$ -parastichy. This last spiral, from  $C_{n+\ell-sk}$  up to  $C_n$ , remains located between the two adjacent  $k$ -parastichies : as a consequence, all circles  $C_{n+jq_{r+1}}$  ( $j = 1, \dots, t$ ) overlap necessarily with those of the two chosen  $k$ -parastichies.

*Proof of theorem 1.* Theorem 1 is a mere corollary of the four propositions stated above !

**Proposition 5.** *The following two equations*

$$F_{q_r}(x, r) = F_{q_{r+1}}(x, z) \quad F_{q_{r+1}}(x, z) = F_{q_{r+2}}(x, z)$$

*admit two and only two solutions, namely  $(x_0, z_0)$  and  $(x_0, 1/z_0)$ .*

*Outline of the proof.* By use of (16), the two equations may be written as

$$\frac{\cos^2 \pi q_r x}{\cos^2 \pi q_{r+1} x} = \frac{\cosh^2 \left( \frac{q_r}{2} \ln z \right)}{\cosh^2 \left( \frac{q_{r+1}}{2} \ln z \right)} \quad \frac{\cos^2 \pi q_{r+2} x}{\cos^2 \pi q_{r+1} x} = \frac{\cosh^2 \left( \frac{q_{r+2}}{2} \ln z \right)}{\cosh^2 \left( \frac{q_{r+1}}{2} \ln z \right)}$$

These equations admit a unique common solution  $(x_0, z_0)$  with  $z_0 \geq 1$  (the demonstration uses the same arguments as the proof of proposition 1). It is immediately verified that, by symmetry,  $(x_0, 1/z_0)$  is also solution. This ends the « proof ».

*Proof of theorem 2.* Theorem 2 is a direct consequence of theorem 1 and of proposition 5.

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