REVIEW ARTICLE

A History of the Study of Phyllotaxis

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The study of the patterns formed by similar units in plants (e.g. leaves, scales, florets) is traced from the first primitive observations in ancient times to the sophisticated studies of today. Mathematics entered into the study early, at first as a way of describing the patterns observed, with Fibonacci numbers and the golden section playing a major role, and later in the construction of models designed to explain their origin. Observation and experiment alternated with theory. Explanations offered alternated between functional and causal. Functional explanations that were at first teleological gave way to those based on the idea of natural selection. Causal explanations alternated between the chemical and the mechanical. New light has been cast on the subject with the realization that phenomena similar to phyllotaxis occur in realms outside of botany. © 1997 Annals of Botany Company

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THE GREAT PERIODS OF THE HISTORY AND SCOPE OF THE REVIEW

Phyllotaxis, a subdivision of plant morphology, is the study of the arrangement of repeated units such as leaves around a stem, scales on a pine cone or on a pineapple, florets in the head of a daisy, and seeds in a sunflower. Remarkably these units often form systems of spirals or helices. As a study of the self-organization of repeated units, it somewhat resembles the study of crystallography. In fact, the objects studied may be thought of as living crystals. However, the fact that they are living and growing adds a further dimension to the subject making it necessary to take into account such things as growth rates, heredity, interaction with the environment, and evolution. Trying to explain the regularity of the arrangements of petals, leaves, etc. has led research workers to incorporate molecular biology, general comparative morphology, and evolutionary theory into their thinking.

The history of the study of phyllotaxis is the history of the ideas of those who proposed them, and the history of the evolution of the ideas in the hands of those who exploited them. It is the history of the recognition of errors made, and their later detection and correction. It is a history of dialectical movement between experimental-observational and theoretical-mathematical viewpoints, between physical and chemical approaches, and the history of great trends initiated by the pioneers.

We have divided the history of the study of phyllotaxis into three periods: (1) the Ancient Period (up to the fourteenth century); (2) the Modern Period (from the fifteenth century to 1970); and (3) the Contemporary Period (from 1970 onwards).

Regarding the Modern Period, Lee and Levitov (1997) proposed 'in a roughly historical sequence, the main logical steps of research into phyllotaxis: (a) discovery of phyllotactic patterns (15th–16th), (b) observation and characterization (16th–18th), (c) geometric modelling (since 18th), (d) experimental studies (since 19th), (e) interpretation and explanation (since the end of 19th)'. Phyllotaxis research during this period was concentrated in France, Germany and the United Kingdom.

Though the Contemporary Period is by far the shortest, it contains at least half of the most meaningful developments in the history of phyllotaxis research, and comprises work by the largest number of research workers. The period is characterized by a worldwide effort to deal in mathematical and physiological depth with the challenges of phyllotaxis. It is there we find the most significant breakthroughs in mathematical phyllotaxis, in multidisciplinary approaches and in the consideration of phyllotaxis-like patterns in phenomena far away from botany.

The study of phyllotaxis has been treated historically in the past, but only briefly. Adler (1974) published a series of short paragraphs, each devoted to a main contributor to phyllotaxis research. Before him, Montgomery (1970) published a history of the origins of the spiral theory of phyllotaxis. This review was devoted to the pioneering works of Bonnet, Martius, Schimper and Braun. Jean (1978, 1984, 1994) has added historical comments and an overview of the history of phyllotaxis research, emphasizing the work of the main individual scientists involved and the

various theories proposed. However, the historical coverage still remains incomplete, and there is scope for considerable expansion of the history of phyllotaxis research.

The main objective of the present review is to propose an introduction to the history of the study of phyllotaxis, and to highlight the necessity of writing a more complete history of this subject in the future; after all it is the oldest branch of biomathematics and is still very active. We have condensed into short sections various aspects of phyllotaxis history, concentrating on particular lines of thought or on selected authors, so that when taken together, they cover the general facets of the subject.

Some readers may find that the mathematical aspects of the history of the study of phyllotaxis are given more importance than the botanical aspects. It is rather that over the years botanists (such as Church, 1904; van Iterson, 1907; Richards, 1951) found that in order to improve our understanding of phyllotaxis it was necessary to elaborate mathematical models based on botanical hypotheses (such as those put forward by the botanists Hofmeister, 1868; Schwendener, 1878; Snow and Snow, 1962). Over the years these pioneers have promoted a global scientific approach where mathematics were finally permitted to take their place in the concert of the disciplines concerned by the challenges of phyllotaxis study. Other readers may find that spiral phyllotaxis is discussed more than other types of phyllotaxis. The situation is that the developers of a more global approach to phyllotaxis had to consider spiral, distichous and verticillate phyllotaxis, and the transitions between these types (as did the experimentalists) but as a variation on the theme of spiral phyllotaxis since this is the most widespread type of phyllotaxis in plants. Finally, we are conscious of omissions, and we regret that some important aspects had to be left out for reasons of space.

VERY OLD SOURCES

Little is known about the Ancient Period which goes back at least to Theophrastus (370 B.C.–285 B.C.) and Pliny (23 A.D.–79 A.D.). Theophrastus, in his *Enquiry into Plants*, says about plants that 'those that have flat leaves have them in a regular series'. Pliny, in his *Natural History*, gives more detail. In his description of oparine he says that it 'is a ramose, hairy plant with five or six leaves at regular intervals, arranged circularly around the branches'. We see from these statements that these ancient naturalists recognized different patterns of leaf arrangement and used this knowledge as an aid in plant recognition. This awareness of patterns in leaf arrangement even found its way into ancient architecture. This can be seen in the carved *Acanthus* leaves on the capital of a Corinthian column which according to architectural historians originated in Assyria or Egypt. Depictions of lotus (called sechen and nennefer in Egypt) and date palm, in Egyptian tombs, give clear indications of pattern recognition (e.g. in the Texts of the Pyramids). This information suggests that the starting point for Greek botany was inherited from these earlier civilizations. This is certainly true for other aspects of Greek science. It is now known that the Ancient Greeks (and Romans) were to some extent custodians of the more highly developed and rather secret science that was especially concentrated in Egypt and Assyria-Mesopotamia. The Greeks borrowed heavily from these sources. All learned individuals of ancient Greece served long probationary periods in the university institutes of Old Egypt, where they imbibed the essentials of their knowledge. Among the greatest of these was the mathematician Pythagoras (6th century B.C.). He waited 12 years to be admitted to one such temple where he then spent 22 years of his life. Similarly, Plato spent 12 years studying in an Egyptian temple. Just as the Greeks are considered by us to be the ancestors of our civilization, the Greeks considered Egypt as the source of theirs. The holistic approach of Pythagoras in all aspects of science is an Egyptian conception. It is stated by some, with rather convincing arguments, that the number τ, so important in phyllotaxis, is inscribed in the Great Pyramid. The Egyptians were great lovers of flowers and skilled observers. Thus, we may suspect that the Egyptians knew more about numbers and patterns in plants (i.e. about phyllotaxis) than is revealed in Theophrastus' much-condensed report of earlier knowledge. This is a conjecture for future historians to examine.

THE FIBONACCI NUMBERS AND THE GOLDEN RATIO

Considerably later in the Ancient Period lived the mathematician Leonardo Fibonacci of Pisa (1175–1240). His book *Liber Abaci* (1202) deals with the well-known problem concerning the monthly growth of a population of rabbits. This was a practical problem raised by Fibonacci's father who was a merchant, and he gave the solution to it: for the months taken in succession he obtained the sequence $< 1, 1, 2, 3, 5, 8, 13, 21, ..., F_k, F_{k+1}, ... >$, where each term after the second is the sum of the two that precede it, and F_k is the kth term of the sequence. These numbers are now called Fibonacci numbers, and the sequence is called the Fibonacci sequence. This sequence was to become of first importance in phyllotaxis. It is possible to generate other sequences similar to the Fibonacci sequence by starting with any two numbers and then using the same addition rule to generate the rest. Among them, the sequences $< 1, 3, 4, 7, 11, ... >$ and $< 2, 5, 7, 12, ... >$ also play a role in phyllotaxis. The golden number $\tau = (\sqrt{5}+1)/2$, which is also important in phyllotaxis study, is mathematically related to the Fibonacci sequence by the formula $\lim F_{k+1}/F_k = \tau$. The observation of this sequence in botany constituted a mystery which served as a main spur to the development of the subject. We can express this mystery by saying that the numbers of spirals in observed systems of opposed families of spirals (as seen in daisies and sunflowers for example) are generally consecutive terms of the Fibonacci sequence. Also, the angle of divergence between two similar units along the so-called genetic spiral (one of the numerous spirals observed in buds and on mature plants) is 137·5°, a value closely related to the sequence by the formula $360° \lim F_{k-1}/F_{k+1}$, and to the golden

number by the formula $360°/\tau^2$, the two expressions being equal.

FIRST STEPS IN THE MODERN PERIOD

Bonnet (1720–1793) is usually credited with initiating observational phyllotaxis. There is a gap of more than 1500 years between his work and that of Pliny. However, in the intervening period Andrea Caesalpino, in his *De Plantis Libri* (1583), reported on the geometrical regularity in leaf distributions. Sir Thomas Browne, in his book *The Garden of Cyprus* (1658), also dealt with this problem. Interestingly both were anticipated by Leonardo Da Vinci (1452–1519), who in one of his notebooks (MacCurdy, 1955) described the same arrangement in cycles of five, and even gave essentially the same explanation put forward by Bonnet. Three hundred years later we read in Montgomery (1970) that, in 1811, Palisot revived the ideas of Bonnet and sought to relate them to his studies on the pith.

Charles Bonnet is responsible for the first serious study of the arrangement of leaves. Part 3 of his book entitled *Recherches sur l'Usage des Feuilles dans les Plantes* (1754) mentions that Sauvages published a memoir in 1743, that distinguished four kinds of leaf arrangement. These he called opposite leaves, whorls of three or more leaves, alternate leaves on opposite sides of the stem, and leaves with 'no constant arrangement'. In 1751 Linneaeus had adopted essentially the same classification. Bonnet commented that he also observed a category of symmetry that seemed to have escaped the notice of Linneaeus and Sauvages, namely a spiral arrangement, which he describes as follows: 'Imagine five vertical lines drawn on a cylindrical stem, with equal spaces between them. Put a leaf at the bottom of the first line. Put a second leaf slightly higher up on the third line to the right or the left. Continue in the same direction, putting the third leaf on the fifth line, the fourth leaf on the second line, and the fifth leaf on the fourth line, completing a cycle of five leaves. The sixth leaf, placed on the first line higher than the fifth leaf, starts a new cycle. In this arrangement there are two complete rotations around the stem between the first and sixth leaves, and the leaves between them divide this amount of rotation into five equal parts, so the angle between consecutive leaves is 2/5 of a rotation, or 144°.' This is the first appearance, in botanical literature, of what came to be known as a genetic spiral. Bonnet offered a teleological explanation for its occurrence. Using Aristotelian terminology, he said that the final cause was to assure that the leaves cover each other as little as possible in order to allow the free circulation of air. Bonnet also mentions another arrangement of leaves in parallel spirals, called to his attention by Calandrini (see Montgomery, 1970). From Bonnet's description of them, these appear to be the secondary spirals now known as parastichies. Bonnet says nothing about their being crossed by another set of spirals going in the opposite direction, although such an opposed family of spirals is now commonly recognized.

At this point Johannes Kepler (1571–1630) enters the picture. Kepler is best known as the astronomer who distilled the laws of planetary motion from Tycho Brahe's measurements thereby paving the way for Newton's law of gravitation. Kepler was fascinated by the number five. He noticed that there are only five regular solids, and that the number five is related to two of them, the dodecahedron and the icosahedron. He knew of the existence of cycles of five leaves spiralling around a stem in plants, and that there are five parts to the seed-bearing core of an apple. He also knew that five is a Fibonacci number. Because the Fibonacci sequence is generated by the simple addition rule we have noted above, he concluded that 'the seeding capacity of a tree is fashioned in a manner similar to the above sequence propagating itself'. Thus, he surmised that the Fibonacci sequence is intrinsically involved in some way in plant growth. His reasoning, of course, was false. The Fibonacci sequence does not propagate itself. It is generated by a simple recurrence relation that is only one of an infinite number of possible recurrence relations. We might, for example, start a sequence, S_n, with $S_1 = 2$ and $S_2 = 7$, and generate the rest by the recurrence relation $S_{n+1} = S_{n-1} + 3S_n$. Obviously this sequence does not propagate itself. It is propagated by the recurrence relation we chose for it. It turns out that Kepler's intuition was better than his logic. The Fibonacci numbers do play a role in the growth of plants, although not in their alleged seeding capacity, and the number five, absent in minerals (the crystallographic restriction) is of great importance in plants.

SYSTEMATIC STUDY BEGINS

The history of mathematical and theoretical phyllotaxis starts half a century later than Bonnet. A new phase in the history of phyllotaxis began in the 1830's with the work of Schimper (1830), Braun (1831, 1835), the Bravais brothers (1837) and Lestiboudois (1848). In their hands, the subject began to develop into a serious scientific discipline combining observational data with theoretical hypotheses and the utilization of appropriate mathematical tools. Its further development took many directions. Some investigators concentrated on making observations and organizing the data. Some performed experiments to see if phyllotactic patterns can be altered by physical or chemical intervention. Theorists alternated between functional explanations (related to environmental determinism) and developmental explanations (related to genetic determinism). After the appearance of Darwin's theory of evolution, teleological explanations were abandoned.

In *Geiger's Magazin für Pharmacie*, Schimper (1830) studied the spiral arrangement of leaves around a mature stem and introduced the concepts of genetic spiral, divergence angle and parastichy. He supposed that all divergences were rational numbers (fractions). He discovered that the most common divergence angles could be expressed by the ratio of two alternate terms of the Fibonacci sequence such as 1/3, 2/5 and 3/8. Like Bonnet before him, he viewed the spiral arrangement as a succession of cycles, with the first leaf of each cycle directly above the first leaf of the cycle that precedes it. Each spiral could be

characterized by two numbers, the number of times it wound around the stem in the ascent from any leaf to the one directly above it, and the number of intervals into which this ascent was divided by successive leaves. Dividing the first number by the second gave the angle between successive leaves, expressed as a fraction of a turn. Schimper called this angle the divergence angle. He noticed that in some cases the fractions were made of alternate terms of other sequences that are generated by the same addition rule as the Fibonacci sequence. The way in which Schimper defined the divergence angle automatically made it a rational number (ratio of two integers). However, he was well aware of the fact that the first leaf of a cycle was not exactly above the first leaf of the cycle that precedes it. He even gave a name to the deviation from exactness. Nevertheless he persisted in using fractions as divergence angles.

Schimper's friend Alexander Braun examined the arrangement of scales on a pine cone. This brought into the picture what are now known as conspicuous parastichies. These are the secondary spirals determined by joining each scale to is nearest neighbour to the right and to the left. A number of parallel parastichies going up to the right are seen to cross a number of parallel parastichies going up to the left. Braun observed that in most cases the two numbers are consecutive terms of the Fibonacci sequence. His explanation for the occurrence of the Fibonacci numbers as numerators and denominators of divergence angles, or as numbers of left and right parastichies was that they appear in the convergents of the simplest of all continued fractions, the one whose terms are all ones. Since this is the continued fraction for the golden section τ, this is how the golden section made its first appearance in the literature of phyllotaxis. Braun's 'explanation' is not really an explanation at all. Nevertheless it had a potential that was later exploited by De Candolle and Coxeter amongst others, as we shall see later.

NEW METHODS OF STUDY INTRODUCED BY THE BRAVAIS BROTHERS

Shortly after the papers by Schimper and Braun were published, Louis Bravais, a physician and botanist, and his brother Auguste Bravais, a naval officer and explorer, published a joint paper entitled *Essai sur la Disposition des Feuilles Curvisériées* (Bravais and Bravais, 1837). They introduced methods of study that have become a permanent part of the tool kit of students of phyllotaxis. They represented leaf distribution as a point-lattice on a cylinder. They recognized that the spirals that catch the eye are secondary spirals. They proved that there is only one genetic spiral if, and only if, the numbers of secondary spirals going up to the right and to the left are relatively prime. If the greatest common divisor of these numbers is $g > 1$, then there are g genetic spirals and there is a whorl of g leaves at each node. For the case of a single genetic spiral, they numbered the leaves in order of appearance, and determined their positions on the secondary spirals. They spoke of visible sets of secondary spirals and used what was essentially a visible opposed parastichy triangle. However, they never defined these concepts precisely, and so drew some unsupportable conclusions. These concepts were clarified only recently (Adler, 1974).

Bravais and Bravais disagreed with Schimper and Braun's use of rational numbers as divergence angles between leaf primordia. Instead they postulated that divergences are irrational numbers (numbers such as $\sqrt{2}$ and τ that cannot be expressed as the ratio of two integers). They claimed that the most common divergence angle is an irrational angle approximately equal to $137°30'28''$ ($360°/\tau^2$) and associated with the Fibonacci sequence. They said that other arrangements were also possible, and they mentioned an irrational divergence angle approximately equal to $99°30'6''$ corresponding to the sequence $< 1, 3, 4, 7, 11, ... >$, and another one of $77°57'19''$ corresponding to the sequence $< 1, 4, 5, 9, 13, ... >$. After the collaboration with his botanist brother in the study of plants (which he then saw as living crystals), Auguste Bravais went on to become one of the founders of the science of crystallography.

Many years later P. G. Tait published a note on the papers of the Bravais brothers in the *Proceedings of the Royal Society of Edinburgh* (1872) describing them as 'terribly elaborate' and complaining that 'these papers certainly cannot be supposed to present the subject from the simplest point of view'. He then set out to put 'the elements of the matter as simply and intelligibly' as he could. Unfortunately his way of simplifying some of the mathematical proofs given by the Bravais brothers was to dismiss many of them as 'obvious' and in many cases he offered no alternative. Tait did propose his own overall interpretation of the situation. This is more clearly expressed in terms introduced recently by Adler (1974). In brief, this interpretation states that if (m, n) is a visible opposed parastichy pair, then so is its contraction $(m-n, n)$ if $m > n$, or $(m, n-m)$ if $n > m$. Applying this contraction procedure repeatedly to the case where m and n are consecutive Fibonacci numbers, the divergence was shown by Tait to lie between $1/3$ and $1/2$. However, Tait also asserted that therefore, if the divergence is between $1/3$ and $1/2$ the visible opposed parastichy pairs must be consecutive Fibonacci numbers. This was an error, since he assumed that the process of contraction is uniquely reversible, but it is not. The reverse of a contraction is an *extension*, and while there is always only one possible contraction, there are always two possible extensions, and each extension entails a restriction of the range of possible values of the divergence. For example, it is true that the opposed parastichy pair $(2, 3)$ is visible if and only if the divergence is between $1/3$ and $1/2$. The two extensions that are possible are $(5, 3)$ and $(2, 5)$. The pair $(5, 3)$ is visible and opposed if, and only if, the divergence is between $1/3$ and $2/5$. The pair $(2, 5)$ is visible and opposed if, and only if, the divergence is between $2/5$ and $1/2$. D. W. Thompson in his influential book *On Growth and Form* (1917) relied entirely on Tait's note, and was misled into concluding that the determination of the precise angle of divergence of two consecutive leaves of the generating spiral does not enter into the above general investigation..., and the very fact that it does not so enter shows it to be essentially unimportant.

THE SEARCH FOR EXPLANATIONS

The first two divergence angles, found by the Bravais brothers to be the most common, can be expressed by a single formula: $d = [1/(t+\tau^{-1})]360°$, $t = 2$, 3, and the numbers of left and right spirals that constitute an opposed parastichy pair are consecutive terms of the particular sequence associated with each of the values of d. The two sequences also have a common property, namely that they are generated by the same addition rule. These two facts immediately raise the question: Why does nature prefer this form for a divergence and this rule for selecting opposed parastichy pairs? A search for an explanation opened a new phase in the history of phyllotaxis research, and is characterized by the construction of theories. These alternated between the developmental and the functional; the developmental theories alternating mainly between the chemical and the physical.

Naumann (1845) described the quincunx arrangement of leaves and introduced a few sequences related to spiral phyllotaxis, particularly on *Echinocactus* (see Jean, 1994). Later Nägeli (1858) gave some ideas on divergence between leaves and on the relationship between spiral and whorled patterns. In 1868, in his *Handbuch der Physiologischen Botanik*, Hofmeister suggested a morphological process that could be responsible for the formation of primordia and their interaction. He proposed that new primordia appear periodically at the apex boundary in the largest available gap left by the preceding primordia. This hypothesis is one of the two used by Douady and Couder (1992) in their numerical simulations of phyllotactic patterns.

In 1878 Simon Schwendener published his book *Mechanische Theorie der Blattstellungen*. In it he proposed the theory that the leaf arrangements result from contact pressure that each growing leaf primordium exerts on its neighbours. To develop his argument he used force diagrams, ruler and compass constructions, and a mechanical apparatus that served essentially as an analog computer simulating the assumed conditions. Unfortunately there was a fallacy in his use of force diagrams. Using the plane development of a cylinder, he represented the girth of the cylinder by a line segment OO′, with a force applied outwards at O, and an equal and opposite force applied at O′. He concluded from this that the girth would expand. He overlooked the fact that O and O′ represent the same point on the cylinder, hence equal and opposite forces on it add up to zero and have no effect at all. However, the empirical observations he made from his constructions and his use of the mechanical apparatus produced remarkably accurate results that were validated almost a hundred years later by rigorous mathematical argument (Adler, 1974, 1977*a*). His results are described most easily in terms commonly used today. Schwendener described what is now known as a conspicuous opposed parastichy pair made up of *m* left parastichies and *n* right parastichies, and referred to as (*m*, *n*) phyllotaxis. Schwendener also observed that as the ratio of the internode distance to the girth of a stem decreases, (1, 2) phyllotaxis gives way to (3, 2) phyllotaxis, which in turn gives way to (3, 5) phyllotaxis, etc. He found that in the course of this advance to higher and higher phyllotaxes, the divergence alternately decreases and increases, with narrower and narrower swings, and converges to the ideal angle $360°\tau^{-2}$. He also measured accurately the limiting angle between which each swing takes place. In conformity with the work of Schwendener, Delpino (1883) formulated a mechanical and physiological theory of phyllotaxis, while Wiesner (1875) returned to the functional explanation of da Vinci and Bonnet that the divergence between consecutive leaves in a spiral arrangement was such that it optimized their access to what they needed for growth, and facilitated transpiration. Since he followed Darwin, his ideas were evolutionary rather than teleological in character. Thus, the trait was explained not in terms of its design for a specific purpose, but as being perfected in its function by natural selection. To support his theory, Wiesner conducted experiments in which he exposed artificial leaves made of litmus paper to light coming from above. He claimed to show that a spiral arrangement with $d = \tau^{-2}$ caused the least shading of the lower leaves by the upper leaves, and thus maximized the amount of light the leaves received. An examination of his data show that they fail to support his conclusions. Nevertheless they were reported in botany textbooks as Wiesner's Law.

Wright (1873), supported Wiesner's Law and produced at least partial confirmation of it when he showed, by means of diagrams, that of all the possible rational divergences whose denominators are less than 14, those that are closest to τ^{-2} give the most open arrangement of leaves. Almost a century later, Leigh (1972) attempted a mathematical proof of Wiesner's Law and Niklas (1988) took a remarkable computerized treatment where a great variety of factors intervene with light. One of his conclusions is that the need for light does not necessarily drive plants to adopt the Fibonacci angle since optimal illumination can be obtained by producing long slim leaves.

In a communication to the Royal Society in 1873, Airy offered a functional explanation of phyllotactic arrangements and shifted attention away from the mature stem to the apex where leaf primordia emerge. He stated that 'in the bud we see at once what must be the use of leaf-order. It is for economy of space, whereby the bud is enabled to retire into itself and present the least surface to outward danger and vicissitudes of temperature'. This idea of packing efficiency was later given an elegant mathematical treatment by Ridley (1982). Airy also proposed the theory that the spiral arrangement of leaves evolved from the alternate order (constant divergence angle of 1/2 or 180°, called distichy today). To demonstrate that this could happen he used a model constructed from a stretched rubber band with small spheres attached to represent leaf primordia. If the rubber band is given a slight twist and is then allowed to contract, the small balls fall into a compact arrangement, and the numbers of parastichies displayed are consecutive Fibonacci numbers. He also observed that 'further contraction, with increased distance of the spheres from the axis' produces parastichies with higher numbers. After the publication of Hofmeister's book and Airy's paper, the study of the leaf primordia in the bud rather than the leaf arrangement on a mature stem became a permanent feature of the study of phyllotaxis.

NO INTERMEDIATE CONVERGENTS: A CLUE TO UNDERSTANDING PHYLLOTAXIS

The botanist De Candolle (1881) looked for a mathematical explanation of the theories of Wiesner and Airy. He pointed out that the continued fractions for divergence angles that actually occur have a common property in that they have no intermediate convergents. This property is a consequence of the fact that, after the initial term that places the divergence between two consecutive unit fractions (fractions whose numerator is one), all the succeeding terms are ones. Quite independently, Coxeter (1972) made the same observation 90 years later. The significance of this may be seen in the recurrence relation governing principal convergents of a simple continued fraction for the divergence angle $d = [a_0; a_1, a_2, a_3, ...]$:

$$p_{n+1}/q_{n+1} = (a_{n+1}p_n + p_{n-1})/(a_{n+1}q_n + q_{n-1}),$$

where $n = 0, 1, 2, 3$ etc. If $a_{n+1} = 1$, this becomes $p_{n+1} = p_n + p_{n-1}$, and $q_{n+1} = q_n + q_{n-1}$. That is, the higher numerators and denominators are obtained by the same addition rule that generates Fibonacci numbers. If from some $i > 0$, $a_i > 1$, then d has intermediate convergents.

This mathematical tool lead to an important improvement in our understanding of phyllotaxis. In the Contemporary Period, the properties of continued fractions in the Bravais cylindrical lattice were thoroughly examined by Adler (1974), Marzec and Kappraff (1983), Rothen and Koch (1989 *a*, *b*), and many others, while Douady and Couder (1992) and Levitov (1991 *a*, *b*) exposed mathematically discontinuities and instabilities that explain transitions between various types of phyllotactic patterns.

REJECTION OF THE MATHEMATICAL APPROACH

After the work of Schimper, Braun, the Bravais brothers, Wiesner and Airy, Sachs' *Textbook of Botany* (1882) exerted a marked influence on the subject and his view constituted the standard for many decades. Sachs' approach was followed in similar vein by Thompson (1917) and Plantefol (1950). Sachs rejected all the mathematical theory of phyllotaxis, stating that this was nothing but a game with numbers, and that the many spirals observed on plants were nothing but an irreducible subjectivity. These negative comments put a brake on the development of theoretical phyllotaxis, and thus in our understanding of phyllotaxis. The work of botanists such as van Iterson, Church and Richards should be regarded all the more highly as they continued to carry the torch of theoretical and mathematical phyllotaxis. Some of the sections below are devoted to their important work. Botanical data on phyllotaxis continued to accumulate; they found their meaning in the theoretical frameworks devised during the Contemporary Period.

Julius Sachs, saw no significance whatever in the continued fractions for divergence angles. Because several different continued fractions had to be used, he saw them as arbitrary

and meaningless *ad hoc* devices. He said, 'since moreover no actual relationship of the method to the history of development, to the classification of plants, or to the mechanics of growth, has been established, in spite of numberless observations, it seems to me absolutely impossible to imagine what value the method can have for a deeper insight into the laws of phyllotaxis'. We cannot but disagree strongly with this judgment, and one of the reasons is that the Fundamental Theorem of Phyllotaxis shows precisely how the divergence and visible opposed parastichy pairs are related. In the advance from lower phyllotaxis to higher phyllotaxis, it is simply the terms of the continued fraction for the divergence that determine the succession of visible left or right extensions that can become conspicuous.

HISTORY OF PHYLLOTAXIS AROUND A THEOREM

In the capitulum of a sunflower there are two opposed families of spirals at the periphery, and two others in the middle and sometimes two other families in between. There are spirals (the parastichies), families of spirals, pairs of families of spirals. In general we find the generative or genetic spiral, contact parastichy pairs (two or three pairs), opposed parastichy pairs (a great number), conspicuous parastichy pairs (one or two pairs), visible pairs, and visible opposed pairs (see Jean, 1994 for definitions). So for an observer there are plenty of reasons to be deterred by this apparent muddle.

Schimper (1830) concentrated on the genetic spiral for his theory of phyllotaxis. Church (1904) favoured the conspicuous pairs and built his equipotential theory around it. Plantefol (1950) concentrated on a single family of spirals, he called foliar helices, which, according to him, are a biological reality. The great merit of Plantefol's analysis was to answer Thompson's objection about the irreducible subjectivity of spirality in plants. The drawback in Plantefol's view is his elimination of mathematics from the analysis of phyllotaxis, and his concentration on only one family of spirals. There is also an internal contradiction in this since even the recognition of a family of spirals constitutes an inherent grasp of mathematics. Given that we can see and count all those spirals mentioned above, foliar helices or not, they all have biological reality.

During the Contemporary Period what was called (Jean, 1984) the Fundamental Theorem of Phyllotaxis (FTOP), first discovered by Adler (1974) answered detractors of the role of mathematics in phyllotaxis. The theorem puts order into the seemingly confusing multiplicity of spirals observed on plants. It is this multiplicity that lies at the centre of the debate. The theorem was formulated in terms of the Bravais and Bravais cylindrical lattice and can be explained by the following working example, which also displays an algorithm (Adler, 1974) for its use.

To find the range of possible values of d for which the opposed parastichy pair (9, 16) is visible, first perform a sequence of contractions until a pair is reached that has the form $(t, t+1)$: the sequence (9, 16), (9, 7), (2, 7), (2, 5),

(2, 3). Write them in reverse order one under the other, and write L or R next to each pair after the first, depending on whether it is a left or right extension of the one that precedes it. The sequence now begins with (2, 3), whose range of possible values of d is [1/3, 1/2] (unit fractions with denominators equal to the numbers in the parastichy pair). At each step, calculate the mediant between the ends of the range (the fraction whose numerator is the sum of the numerators, and the denominator is the sum of the denominators). The mediant divides this range into two intervals. In the next step, the range is the left interval if that step is a left extension, and it is the right interval if that step is a right extension:

Type of extension	pair	range of d	mediant
	(2, 3)	[1/3, 1/2]	2/5
R	(2, 5)	[2/5, 1/2]	3/7
R	(2, 7)	[3/7, 1/2]	4/9
L	(9, 7)	[3/7, 4/9]	7/16
R	(9, 16)	[7/16, 4/9]	

Mathematically the theorem can be summarized in the following way: (a) there is a natural division of the interval [0, 1/2] (the range of possible values of the divergence angle d) into sub-intervals bounded by consecutive unit fractions [1/($t+1$), 1/t], $t = 2, 3, 4$, etc.; (b) the opposed parastichy pair (t, $t+1$) is visible if, and only if, $1/(t+1) \leqslant d \leqslant 1/t$; (c) if ($p$, q) is a visible opposed parastichy pair with p and q relatively prime, then there is a unique value of t such that (p, q) can be obtained from (t, $t+1$) by a sequence of left and right extensions; (d) at each step in the sequence of extensions to reach (p, q), the range of possible values of d is made smaller according to the rule illustrated above.

Historically, the Fundamental Theorem of Phyllotaxis was presented in the context of an analysis of Schwendener's contact pressure model enhanced by further clarification of basic concepts (Adler, 1974, 1977) that distinguished between an opposed parastichy pair, a visible opposed parastichy pair, and a conspicuous parastichy pair. To eliminate size as a factor, since it is known to be irrelevant, a normalized cylindrical representation was used in which the girth of the cylinder is taken as unit of length. The vertical component of the distance between two consecutive leaves on the genetic spiral has been called the 'rise, r'. Adler studied the consequences that flow from two assumptions: (1) there is a period in the growth of the plant when the rise, r, is decreasing (that is, when the girth is growing faster than the internode distance); and (2) there is a period when the minimum distance between leaves is maximized. Adler showed that during the time when these two periods overlap, the divergence, d, oscillates, alternately decreasing and increasing, with smaller and smaller swings, and converges toward a limiting value. If maximization of the minimum distance begins early (as defined in his paper), then this limiting value is τ^{-2}. He also demonstrated rigorously that maximization of the minimum distance requires that the two leaves that are nearest neighbours to any leaf must be equidistant from it, and this in turn requires that the advance to higher phyllotaxis as r decreases must follow the addition rule that generates Fibonacci-like sequences. Two important by-products of this work are a mathematical proof of the Fundamental Theorem of

Phyllotaxis, and a clarification of the role of the continued fraction for the divergence. This demonstrates that the opposed parastichy pair (t, $t+1$) is visible and opposed if, and only if, $1/(t+1)/ \leqslant d \leqslant 1/t$, and if $d = [0; t, a_2, a_3, …]$ (the continued fraction for the divergence angle d), then $a_2 - 1$ right extensions are visible, followed by a_3 visible left extensions, a_4 visible right extensions, a_5 visible left extensions, etc. A special case of the theorem is that the parastichy pair (F_k, F_{k+1}) is visible and opposed if, and only if, the divergence angle d is equal to F_{k-2}/F_k or to F_{k-1}/F_{k+1} or is between these two values. A more particular formulation of the FTOP is given in the section entitled 'New methods of study introduced by the Bravais brothers'.

The Fundamental Theorem of Phyllotaxis was reworked by Jean (1984), and was given a specific formulation, various applications and an intuitive presentation; simple algorithms were proposed to obtain intervals for divergence angles from visible opposed parastichy pairs observed and *vice versa* (Jean, 1994). Goodal (1991) referred to the Fundamental Theorem as the Adler-Jean theorem. The theorem has been proved and used by crystallographers who came to the study of phyllotaxis in the late 1980s.

Jean's Dynamic Model $r = (m+n)^{-2} \ \tau^3(\sqrt{5}\cot\gamma + \sqrt{(5\cot^2\gamma+4)})/2\sqrt{5}$, essentially completes the Fundamental Theorem (Jean, 1994). The rise, r, is implicitly linked to the divergence angle, d, by the FTOP, and to Richards's famous plastochrome ratio R; γ is the angle of intersection of the opposed pair (m, n) of m and n spirals. The Dynamic Model brings together the prominent parameters used in phyllotaxis. It allows patterns in phyllotaxis to be recognized easily, accurately and efficiently (Jean, 1994, chapters 4, 5) by experimentalists and observers. From all possible combinations of observed parameters, the other parameters can be obtained from a 'Pattern Determination Table' that has been built from the model. In particular, the angle γ which was not given by previous models can be obtained from the Table. With the model we can also link the pair (m, n) with Church's bulk ratio, Richards' area ratio, and the plastochronic time, and we can even deal with the global form (width and length) of a phyllotactic organization (see Barabé and Jean, 1996). Phase diagrams can be built to show the behaviour of the parameters involved, and these diagrams may be compared to those of van Iterson introduced below. It is precisely the absence of such clarifying mathematical tools which drove Sachs and Thompson to their negative demobilizing conclusions.

CHURCH'S IDEAS AND THE CENTRIC REPRESENTATION

In the first half of the 20th century we meet three other pioneers whose findings and approaches are of great importance in the development of the subject. They are Church (1904), van Iterson (1907) and Richards (1948). With the secret of phyllotaxis assumed to be hidden in the growing tip of the stem, a new technique for studying it, first proposed by Church (1904), was introduced. The tip was cut

at right angles to the axis, and drawings were made of the spirals revealed. This became known as the centric representation. Church and Richards worked mainly in the centric representation of phyllotaxis in which many models were formulated during the Contemporary Period.

Church's published works incorporate a gold mine of illustrations of phyllotactic patterns, and propose a still plausible explanation of the phenomenon of transitions between the patterns. This phenomenon raises theoretical and experimental questions, especially the one of discontinuous transitions. In that case, one observes changes such as $(m, n) \rightarrow (m, n-1)$ and $(m, n) \rightarrow (m-1, n)$. Although this phenomenon has been scrutinized and illustrated by many authors (e.g. Fujita, 1942; Meicenheimer and Zagorska-Marek, 1987; Zagorska-Marek, 1994), it has not yet been fully incorporated in theoretical models of phyllotaxis. For example, the discontinuous transition from decussation to spiral pattern raises many morphological and theoretical questions which though studied from descriptive (Guédès and Dupuy, 1983), experimental (Meicenheimer, 1982, 1987) and theoretical (Douady and Couder, 1996) points of view, constitute an open problem for botanists as well as for mathematicians.

Church also proposed the idea that parastichies are lines of force, and that undulating cellular masses with different wavelengths produce the patterns of parastichies. He put forward a mathematical treatment of these ideas. Church is also responsible for dealing with the phylogenetic aspect and the deep evolutionary causes of pattern formation in phyllotaxis, a point of view used and developed later by Jean (1994, 1997) in an entropy-like model of phyllotaxis. Church replaced the cylindrical picture with the concept of leaves as points inside a disc. He rejected the idea of a fundamental spiral and insisted instead that parastichies are fundamental. He put forward the theory that impulses of energy travel away from the centre of the disc in spiral paths, and that new leaves grow where the spirals intersect. By rejecting the simple cylindrical representation in favour of the disc (centric) representation, Church transformed simple geometric relationships into seemingly complicated ones (because of the presence of the logarithmic function), and thus made them more difficult to discover. In truth, the two representations are mathematically equivalent. Church's centric representation can be obtained from Bravais' cylindrical lattice and *vice versa* by a simple logarithmic or exponential transformation. By rejecting the fundamental spiral in favour of parastichies Church blinded himself to the fact that the existence of each implies the existence of the other. Thus, his work includes some confusions and errors as well as significant ideas. But, we must note that even if the centric representation does not take into account the three-dimensional aspect of a growing apex, it is still very useful in empirical studies, particularly for calculating phyllotactic parameters on microscope slides (e.g. Rutishauser, 1982).

Church's contributions were ignored for decades. It is Richards (1948) who gave Church's mathematical treatment the required attention, which has subsequently been refined (see Thornley, 1975; Jean, 1994, part I). Today, those who study the sunflower with state-of-the-art computer tools in

centric representation have amplified Church's ideas (e.g. van der Linden, 1990, 1996). Almost one century after Church, Green (1992) came to Church's ideas about undulating masses of cells in the plant apex, and linked phyllotaxis to the physics of metal plates by considering Chai's diagram of 'decussation' reproduced with bulging plates subjected to stresses. Douady and Couder (1992) who reproduced phyllotactic patterns by means of droplets of ferro-fluid in a magnetic field, remind us of Church's idea that parastichies could be lines of force and equi-potential, although they put the lines of force elsewhere.

A COMMENT ON RICHARDS' CONTRIBUTION

Following in the path of Church, Richards (1948) displayed a leaf distribution as a set of points in a disc. He introduced the term *plastochrone ratio* for the ratio, R, of the distances of two successive leaves from the centre of the disc, and derived a formula relating this ratio to the number of parastichies that are most conspicuous (the rise, r, mentioned earlier is related to Richards' plastochrone ratio by the formula $r = \ln R$). In Richard's system (1951) three parameters are necessary for a complete mathematical description: the angle of the cone tangential to the apex in the region under consideration, the divergence angle and the plastochrone ratio. The plastochrone ratio, R, is rendered more useful by transforming it to the related concept of the phyllotaxis index, defined as $0.38 - 2.39 \log_{10} \log_{10} R$. The constants in the definition are chosen so that successive integral values of the index correspond to successive orthogonal pairs of conspicuous parastichies expressed by consecutive terms of the Fibonacci sequence. Richards' index is still currently used for the description and quantitative analysis of phyllotaxis (Williams, 1975; Rutishauser, 1982). Despite Richards' statements that a theory of phyllotaxis must be independent of any particular assumption, his phyllotaxis index is constructed on the Fibonacci sequence, and is not of help for the many other systems expressed by other sequences. It appears that the use of Richards' third parameter for describing phyllotaxis in three-dimensional space does not add much to the precision of the characterization of patterns based on R and d only. Though being biologically a three-dimensional phenomenon, practically speaking phyllotaxis can be rightfully studied, without loss of relevant information, as a two-dimensional phenomenon. During the sub-period from 1945 to 1960, Richards' mathematical work partially counter-balanced other strictly botanical studies. Richards (1948, 1951) favoured Schoute's hypothesis that the placement of primordia was determined by a chemical inhibitor, and he called it a 'field theory' although he never produced any field equations.

CHEMICAL THEORIES

Theorizing about phyllotaxis took a new direction with the work of Schoute (1913). In his paper *Beitrage zur Blattstellungslehre* he surveyed the literature on the subject

and came to the following conclusions: (1) the dominance of the principal series (the Fibonacci sequence) over parastichy numbers and the divergence is still unexplained; and (2) the direction in which a solution should be sought is the one taken by Schwendener (1878). However, there is a gap in the work of Schwendener in that he does not explain the initial placement of primordia. To fill this gap, Schoute proposed the theory that the initial placement is determined by a chemical inhibitor secreted by each primordium that prevents a new primordium from emerging too close. This theory was dominant during the first half of the twentieth century. A similar chemical theory was put forward by Turing (1952). He suggested 'that a system of chemical substances called morphogens, reacting together and diffusing through a tissue, is adequate to account for the main phenomena of morphogenesis'. He studied in detail the case of an isolated ring of cells and wrote as follows: 'the investigation is chiefly concerned with the onset of instability. It is found that there are six essentially different forms which this may take. In the most interesting form stationary waves appear on the ring. It is suggested that this might account, for instance, for the tentacle patterns on *Hydra* and for whorled leaves'. Later, other models of diffusion were formulated including those by Schwabe and Clewer (1984) and by Chapman and Perry (1987). Meinhardt's (1984) approach, with equations controlling the diffusion of morphogens, also gave meaningful results. But to date it is still not known whether such morphogens or inhibitors exist. Richards (1948) and Wardlaw (1949) found support for the inhibitor theory in the experimental work of Snow and Snow (1931).

EXPERIMENTS IN PHYLLOTAXIS

There is an extended history on the dialectical movement between observation-experimentation and mathematics-theory-modelling. Mary and Robert Snow initiated an experimental phase of the study of phyllotaxis. They studied the effect of isolating a leaf primordium of *Lupinus albus*. They concluded (Snow and Snow, 1931) that the position at which a new leaf primordium is initiated is influenced by the pre-existing leaf primordia adjacent to the site of initiation. They, and others after them, showed that the phyllotaxis of a growing plant can be altered by surgical or chemical intervention. For example, Wardlaw (1949) used surgical techniques to study the phyllotaxis in the fern *Dryopteris*. He suggested an inhibitory effect upon young primordia by older adjacent primordia. But the Snows (1962) interpreted these results differently; they proposed the theory that 'each new leaf is determined in the first space on the growing apical cone that attains a necessary minimum size and minimum distance below the tip'. This hypothesis was used by Douady and Couder (1996) in their recent theoretical model of phyllotaxis. In the 1960s, surgical experimentations in the plant apex were used extensively by the *Ecole de Morphologie Française* following-up Plantefol's theory of foliar helices (Loiseau, 1969).

On the experimental, anatomical and physiological aspects of phyllotaxis, we find compilations by Cutter (1965), contributions by Wardlaw (1965), and a book by Loiseau (1969) mainly recapitulating Plantefol's theory (1948) of foliar helices. The tradition of conducting experiments in phyllotaxis is alive and well. Particularly noteworthy is the work of Erickson and his students. Among them Meicenheimer (1981, 1982) studied changes in *Epilobium* phyllotaxis induced by chemical substances in relation to the model of van Iterson. Battjes, Vischer and Bachmann (1993) have shown that the Asteracean flower-heads exhibit some of the ring-like properties postulated by the collision model of Hirmer (1931). Green, Steele and Rennich (1996) have demonstrated that physical stress is capable of producing waves similar to those attributed to morphogens by Turing. But another step in the history of experimental phyllotaxis was reached recently when molecular biologists identified genes that promote a change in phyllotaxis from spiral to whorled in *Anthirrhinum* (Carpenter *et al.*, 1995). Distichous, verticillate and decussate phyllotaxes are common, and have been mainly studied from a morphological and experimental point of view (Williams, 1975; Charlton, 1978, 1993; Rutishauser, 1986; Green 1987); they raise many developmental questions which are addressed in the works of Green *et al.* (1996) and Douady and Couder (1996).

THE TREND INITIATED BY VAN ITERSON

In 1907 van Iterson constructed a model in which he assumed close packing of leaf primordia around a cylinder. It is not difficult to show that contact pressure caused by growth and close packing produce the same results. Unfortunately, van Iterson's fundamental analysis of phyllotaxis remained unrecognized for more than 50 years. His work was re-discovered and extended by Erickson (1973). Van Iterson proposed the following equation:

$$\cos(m\alpha/2)/\cos(n\alpha/2) = D^{(n-m)/2}(1+D^m)/(1+D^n),$$

where α is the divergence angle in radians, and D is the diameter of the spheres inserted around a cylinder of diameter 1. Erickson (1983) cleverly used the equivalent formula for practical pattern recognition;

$$\cos(m\alpha/2)/\cos(n\alpha/2) = \cosh(m\ln D/2)/\cosh(n\ln D/2)$$

where cosh is the hyperbolic cosine. These equations have no elementary solution, hence are solved by a sequence of approximations. From his equation van Iterson produced a phase-space diagram showing the relationship between parameters d, b (that is $1/R$) and (m,n). This phase-space diagram can be considered the symbol of modern phyllotaxis. Some years later, Veen and Lindenmayer (1977) constructed a model relating the geometrical parameters of van Iterson to the concept of chemical gradients and obtained a phase-space diagram similar to that of van Iterson. The model of Veen and Lindenmayer represents real progress in modelling phyllotaxis, because it contains a temporal factor (time), in addition to the geometrical parameters. Van Iterson was aware of the fact that what Adler called a visible opposed parastichy pair played a special role in phyllotaxis (he called them 'konjugierte').

However, not having the concept of 'extension' of a visible opposed parastichy pair, he could not, and did not, ask and answer the question: 'when is an extension of a visible opposed parastichy pair also a visible opposed parastichy pair?'

In line with van Iterson's model, physicists (e.g. Levitov, 1991*a*, *b*; Douady and Couder, 1992) have recently taken a further crucial step in the development of our understanding of phyllotaxis. Instead of using geometrical criteria to explain the position of newly formed primordia, they used criteria based on the principle of minimal energy. For them, new primordia tend toward positions where the potential energy is at a minimum. Levitov, and Douady and Couder, obtained phase-space diagrams that are very similar to those of van Iterson. But there is an essential and important difference. In van Iterson's diagrams, there is no discontinuity. Two continuous lines originate from each bifurcation point. In the diagrams founded on the principle of minimal energy, there is a discontinuity at each bifurcation point. The general tendency in the modelling work is to use more and more general principles in order to deal with the fact that we find phyllotaxis-like patterns outside botany and outside biology where there are no genes.

'PHYLLOTACTIC PATTERNS' OUTSIDE BOTANY

The patterns characteristic of shoot phyllotaxis are also found elsewhere (Jean, 1994). Frey-Wyssling (1954) mentioned that similar patterns exist in polypeptide chains. Erickson (1973) developed this observation further by showing how van Iterson's equations could be used to calculate the parameters of microscopic biological structures assembled from protein monomers in helical arrangements. Adler (1977*b*) showed that the equations derived from his model provide a simpler route to these calculations, and are more inclusive in that they cover the double-contact case as well as the triple-contact case. The arrangements of amino-acid residues in polypeptide chains can be predicted using the methods of phyllotaxis (Jean, 1994, chapter 10). Similarly, Levitov (1991*a*, *b*) found 'phyllotactic patterns' in a flux lattice of a superconductor and explained them as a tendency towards minimizing the energy of the system. Douady and Couder (1992) produced phyllotactic patterns in a laboratory experiment with drops of ferrofluid dropped periodically at the centre of a dish, where, as magnetic dipoles, they repelled each other. They found that, as in Adler's model, the divergence angle oscillated while converging to the golden angle. An interesting feature of Levitov's work is his use of the fact that possible paths of the state of the system in the relevant phase space under the conditions of the experiment are arcs of geodesics found in the Poincaré model of the hyperbolic plane (see also Marzec, 1997). The analogies with phyllotactic patterns in general comparative morphology lead directly to the consideration of phyllotaxis from a systemic standpoint where elementary laws of growth (e.g. branching, allometry, gnomonic growth) found generally in nature, play a prominent part.

A SYSTEMIC APPROACH TO PHYLLOTAXIS

The nineteenth century saw the emergence of an entirely new approach to phyllotaxis which had been forgotten for decades, while researchers concentrated on contact pressure and field theories. Lestiboudois (1848), and after him Bolle (1939), linked phyllotactic patterns to the phenomenon of ramification and branching. This led to the construction of a new kind of functional model (Jean, 1980, 1994, 1997) where the growth of leaf distribution is viewed as a succession of cycles, each an extension of the preceding one by the addition of new leaves. Within each cycle, the leaves are ordered as in their projections on the horizontal axis. The cycles are then joined to each other to form a tree diagram with single and double nodes only (for biological reasons). The diagram is called a *hierarchy*. The hierarchies are generated from sets of symbols by using specific rules (the botanist Lindenmayer's systems) given in terms of growth matrices. An entropy-like function can then be defined on the set of hierarchies representing the various phyllotactic patterns, and, using a principle of optimal design, the cost of each type of spiral pattern may be calculated. Among the outcomes of the model, the hierarchy associated with Fibonacci phyllotaxis has minimal cost. The different types of spiral phyllotaxis can be ordered according to increasing costs, multijugacy is seen to be the unifying concept for all types of regular patterns including whorls (verticils), and a terminology is proposed to identify the various patterns. Moreover, the model allows difficult problems of growth to be solved, permits data to be organized (see Barabé and Vieth, 1990), and helps make predictions which can be compared to observations.

If the maximization of the minimal distance between leaves begins early, then Fibonacci phyllotaxis is inevitable (Adler, 1974). This important result is recaptured from the entirely different setting proposed in Jean's entropy-like model, which points to the skeleton of the process being responsible for phyllotactic organization (i.e. branching). It stresses Lestiboudois-Bolle's idea that the basic mechanism is one of growth centres that are bifurcating or not, as in the growth of algae. Church advised us to look at the problem from this standpoint. Branching in phyllotaxis is a subject also dealt with recently by Sattler (1997). Given that phyllotaxis-like patterns are found outside botany, the Jean model also stresses the importance of relying on elementary laws common to botanical and non-botanical examples to explain phyllotactic patterns in a systemic manner (see Jean and Barabé, 1997).

The basic assumptions in Adler's model (1974; that is maximization of the minimum distance between primordia), in Douady and Couder's model (1992; that is the principle of minimal energy, a transposition in physical terms of the biological hypothesis of Hofmeister or Snow and Snow), in Jean's model (1980, 1994 Part II; that is the minimization of an entropy-like function under some constraints), and in Levitov's model (1991*a*, *b*; that is the maximization of the energy of repulsion), are likely to be mathematically equivalent. A proof of this would be a valuable contribution to the theory of phyllotaxis.

CYCLIC HISTORY OF PHYLLOTAXIS

We now propose a retrospective of the history of phyllotaxis from an unusual viewpoint, based on the recognition of cycles. There are cycles not only in nature, but also in the growth of knowledge. What appears as a disconnected succession of events is sometimes a complete and coherent cycle. Old ideas come back in strength after a cycle comprising many periods or sub-periods. We can compare the evolution of knowledge to the way the flying-ant approaches a source of light. Because of the conformation of its eye it describes a logarithmic spiral while it flies around the source. Cyclic pulsation is not only fundamental in the evolution of the universe, but also in the development of knowledge.

During the Contemporary Period, the old ideas of Bravais and Bravais flourished, since most of the mathematical models were formulated in their cylindrical representation using continued fractions. What permitted the revival of Bravais and Bravais' ideas was the dead-end in which the subject found itself in the 1960s, and the considerable progress that sciences complementary to phyllotaxis experienced since the Bravais' time. Crystallographers also incorporated these ideas into their work in the 1980s. The Bravais brothers constituted a multidisciplinary team. Their ideas were set aside as early as the 1840s, but in the Contemporary Period the study of the subject became multidisciplinary again. In fact, we can speak of the Bravais and Bravais cycle in phyllotaxis.

In the area of phyllotaxis, we can put in evidence a cycle of about 160 years, corresponding more or less to the history of mathematical phyllotaxis, and covering the Modern and Contemporary Periods. Its point of departure is the complex of ideas put forward by Bravais and Bravais. Auguste Bravais discovered the crystal lattice and created the reticular language to express crystal structures and phyllotactic patterns. The Bravais brothers proposed an original approach to phyllotaxis, which included the introduction of the cylindrical representation of phyllotactic patterns, and of irrational divergence angles (numbers that are not simple fractions); they recognized the implicit importance of the triangle of opposed parastichies (defined by Adler, 1974), underlined the importance of continued fractions in the area, pointed out the multidisciplinarity of the challenge, and constituted a team in the modern meaning of the term, using the resources of mathematics, botany, physics and crystallography.

After the Bravais brothers, those who dealt with phyllotaxis ceased to refer to crystallography. The public marriage between the two disciplines, botany and crystallography, was doomed to a short public life, but their relationship continued to mature behind the scenes, in obscure publications. Wulff (1907) stated, confidently, that the distribution of floral and foliar nodes is comparable to a crystal lattice. Jaeger (1925) highlighted the similarities between animal, plant and mineral symmetries. Doffin (1959) asserted that it is the phyllotactic lattice which drove Auguste Bravais to conceive of the invisible crystal lattice. Doffin drew attention to the manifestations in the living world of the fundamental property of crystals, namely, periodicity.

He criticized those who created a sterile absolute wall between animate and inanimate worlds. He firmly stated the idea that the domain of phyllotaxis cannot be erected without the active participation of crystallographers. He predicted that crystallographers would soon come to the study of living beings, which he said are so regular. This is precisely what happened in the middle of the 1980s in the area of phyllotaxis, following the discovery of quasi-crystals with pentagonal symmetry (Nelson, 1986) that we believed to be absent from the world of crystals, and which is so important in phyllotaxis. The animate and inanimate worlds started again to illuminate each other.

The theoretical and mathematical approach of the Bravais brothers was marginalized at first because their ideas were in advance of their time. Many other ideas were then tried by other research workers (e.g. the approach with diffusion equations). In the Contemporary Period we came back to the ideas of the Bravais brothers, which were strongly developed, starting with the mathematical (Adler, 1974, 1977a; Coxeter, 1972), and ending with exotic crystallography. The small step along the endless spiral of knowledge appeared to be a considerable step in our understanding of the phenomena of phyllotaxis, the most significant in the history. From the beginning the two brothers appear to have placed the study of phyllotaxis on a fertile track (a biography of Auguste Bravais is now available, Reynaud, 1991).

A SHORT, BUT MEANINGFUL, PERIOD OF HISTORY

The study of phyllotaxis was revitalized at the beginning of the 1970s by North Americans. While in the Modern Period the study of phyllotaxis was made mainly by botanists in Germany, France and the United Kingdom, during the Contemporary Period the study of phyllotaxis became multidisciplinary and marked the renewal of the subject in several other countries. Mathematical phyllotaxis, relatively underdeveloped until then, was given great attention. Landmark publications in mathematical phyllotaxis include those of Coxeter (1972), Adler (1974, 1977a), Thornley (1975), Williams (1975), Ridley (1982), Erickson (1983), Marzec and Kappraff (1983), Jean (1984, 1994), Jean and Barabé (1997) and Thornley and Johnson (1990). Notable contributions by crystallographers include those of Rivier (1986, 1988), Mackay (1986), and Rothen and Koch (1989a, b) who compared phyllotactic patterns with crystals. Physicists also became involved (Bursill, 1990; Douady and Couder, 1992; Levitov, 1991a, b). Among the most worthwhile contributions are those by Meicenheimer (1982, 1987), Rutishauser (1982), Carr (1984), Schwabe (1984), Roberts (1987), Zagorska-Marek (1987, 1994), Niklas (1988), Palmer and Hernandez, (1988a, b), Bursill and Xu Dong (1989), Lyndon (1990), Sattler (1990, 1992), van der Linden (1990), Green (1991, 1992), Ryan, Rouse and Bursill (1991), Dixon (1992), Battjes et al. (1993) and Green et al. (1996). We cannot do justice to all their fine contributions in the present review, due to space constraints. Given that phyllotaxis has become a systemic quest reaching far beyond the realm of botany itself, it is also necessary to mention

some 'outsiders' whose contributions throw light and perspectives on the challenges of phyllotaxis, such as Lima-de-Faria (1988) a molecular geneticist, and Selvam (1990) a meteorologist.

CONCLUSIONS

Immanuel Kant once wrote: 'I assert only that in every particular Nature-study, only so much real science can be encountered as there is mathematics to be found in it'. Using this criterion, we can say that the study of phyllotaxis has now matured as a science. Mathematics has now entered into the study of phyllotaxis in a variety of ways. Many branches of mathematics have been used, including statistics, calculus, differential equations, analytic geometry, linear algebra, number theory, and even hyperbolic geometry. Familiarity with mathematics has become a must for botanists interested in plant morphogenesis. In the area of phyllotaxis, mathematicians, physicists, crystallographers, and others, must marry their expertise with that of botanists who provide at least the basic ingredients for theoretical developments. There is now a dialectical movement between observations and theoretical developments. It is clear that the systemic approach (the global perception of large-scale systems) is the tao of the future, favoured from the beginning by the Bravais brothers.

It is natural to ask what directions the study of phyllotaxis will take in the future. We cannot answer this question with confidence. Genes undoubtedly play a part in the synchronization of the various growth rates found in various models of phyllotaxis. Techniques of genetic analysis and recombination now available may be able to identify these genes and determine their function. But, given the fact that 'phyllotactic patterns' are found elsewhere than in botany, the question is raised about uniqueness of the role of genes.

The history of the study of phyllotaxis that we have constructed proposes a general view under three great periods, the Ancient Period (up to the 14th century), the Modern Period (15th century to 1970), and the Contemporary Period (post 1970). We have shown that there are many complementary ways to look at phyllotaxis. Although our history remains incomplete, some dominant lines that may lead to a more complete understanding have been identified. These are considerations of energy, entropy and lines of force, taking into account environmental and genetic determinisms, using multidisciplinarity, comparative morphology and evolutionary theories. By looking at the past we hope to have awakened the reader's interest in the history, as well as in phyllotaxis research. We believe that the knowledge of phyllotaxis will have practical applications. At least phyllotaxis is now a main strand of bio-mathematics, and there are already applications in other areas of science, of the methods used in phyllotaxis.

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