

Phyllotaxy

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Phyllotaxy (phyllotaxis) is the mode of arrangement of leaves, scales, or bracts with flowers along the plant stem. Phyllotaxy research deals with the study of biological pattern formation (morphogenesis); it answers questions such as what the shoot apical meristem (SAM) does and how it does it.

Introduction

Most phyllotactic patterns originate from a lens-shaped or hemispherical shoot apical meristem (SAM), while the leaves are formed in acropetal and often regular sequence (Figures 1, 2 and 3). SAMs are groups of pluripotent cells responsible for making leaves, stems, and (in seed plants) also flowers. Most SAMs of vascular plants are quite small ($\sim 50\text{--}150\ \mu\text{m}$ in diameter). The largest SAMs are found in cycad stem tips and sunflower capitula with diameters of 2–3 mm.

All regular phyllotactic patterns can be described by connecting neighbouring leaves with curved lines (parastichies) or straight lines (orthostichies). Parastichies and

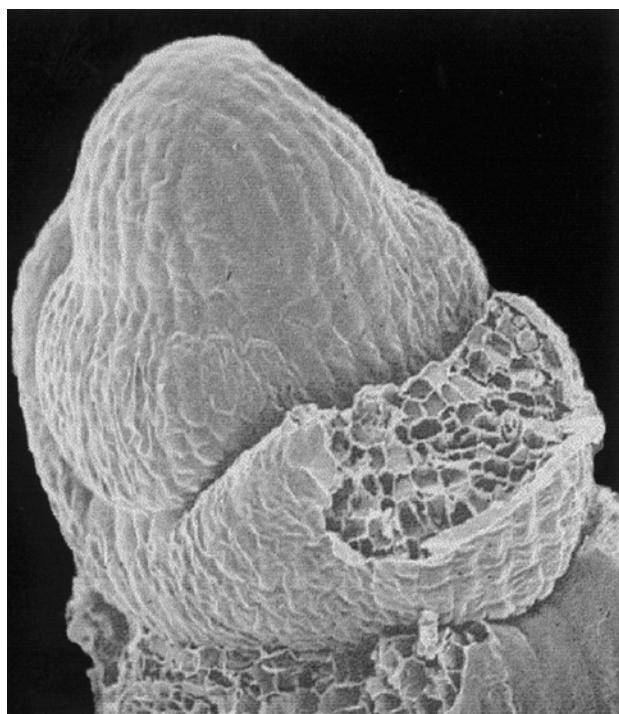


Figure 1 Shoot tip of a member of the carnation family (*Honkenya peploides*), showing decussate phyllotaxy, i.e. crossed leaf pairs. Leaf primordia arise pairwise and opposite each other on the flank of the shoot apical meristem (diameter 150 μm).

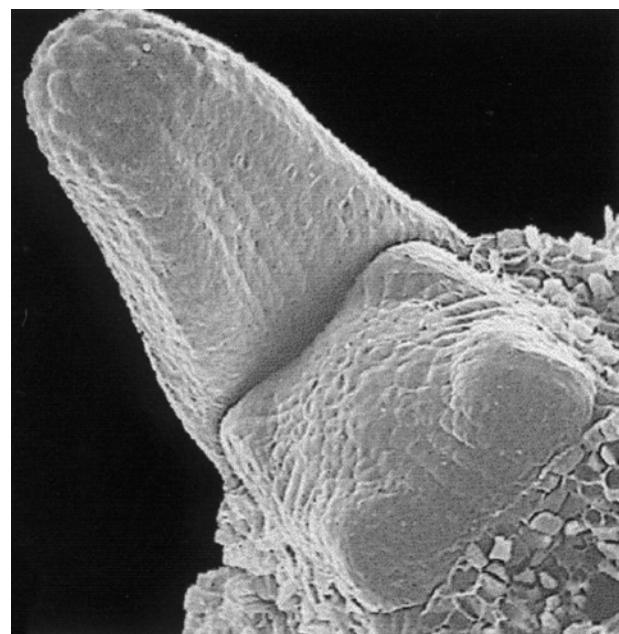


Figure 2 Shoot tip of a shrubby plantain (*Plantago webbia*) with tetramerous whorls. Four leaf primordia are equally distributed around the shoot apical meristem (diameter 80 μm). The leaves of the next older tetramerous whorl are removed except one.

Introductory article

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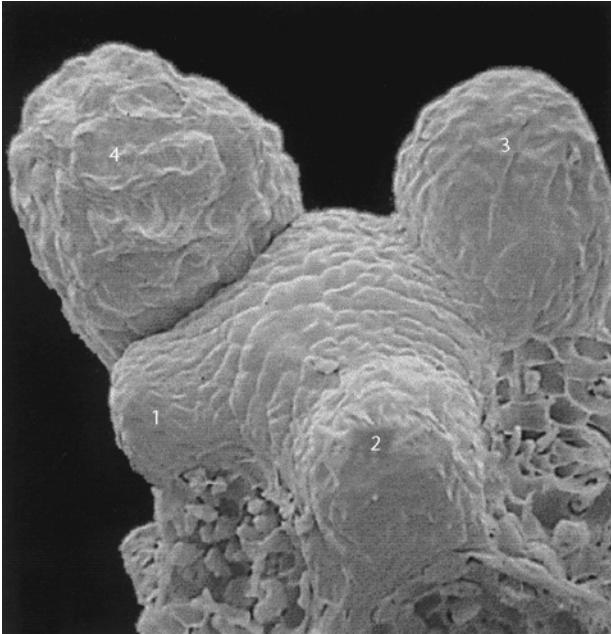


Figure 3 Shoot tip of a yellow stonecrop (*Sedum sexangulare*), showing spiral pattern according to Lucas phyllotaxy with divergence angle approaching 99.5° . Four successively formed leaf primordia surround the shoot apical meristem (diameter $80\ \mu\text{m}$).

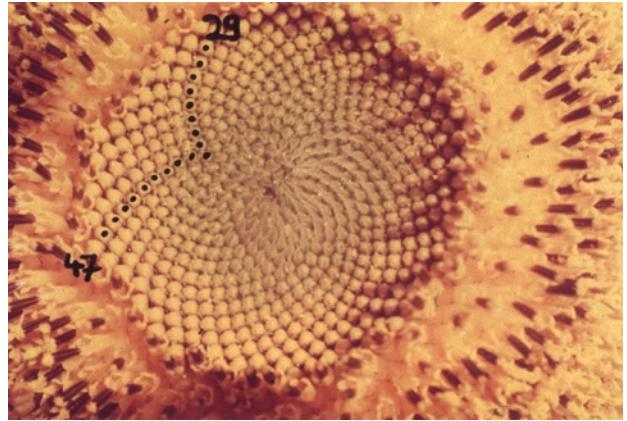


Figure 5 Central portion of sunflower (*Helianthus annuus*) capitulum, with 29 left-turning contact parastichies and 47 right-turning contact parastichies. One of each set is marked with black dots. The contact parastichies [29 + 47] are members of the Lucas sequence 1, 3, 4, 7, 11, Lucas phyllotaxy occurs in $\sim 5\%$ of all sunflower capitula, whereas Fibonacci systems are much more frequent.

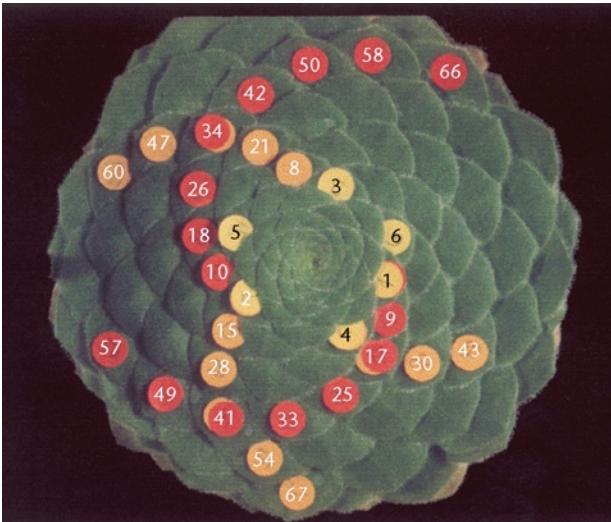


Figure 4 Rosette (diameter 30 cm) of Canarian house-leek (*Aeonium tabuliforme*) representing a Fibonacci system with 8 left-turning contact parastichies (two of them marked with red stickers) and 13 right-turning contact parastichies (three of them marked with orange stickers). Six leaves (1–6) close to the centre are marked with yellow stickers according to the genetic spiral (divergence angle approaching 137.5°).



Figure 6 Pine-cone (*Pinus nigra*) seen from the base, representing bijugate phyllotaxy, another rare spiral system. There are paired scales that are opposite each other or nearly so (labelled with the same even numeral). Consecutive leaf pairs (0–2–4–6– ...) are twisted $\sim 69^\circ$, i.e. the half Fibonacci angle. This rare spiral pattern shows contact parastichies [6 + 10], which are members of the sequence 4, 6, 10, 16,

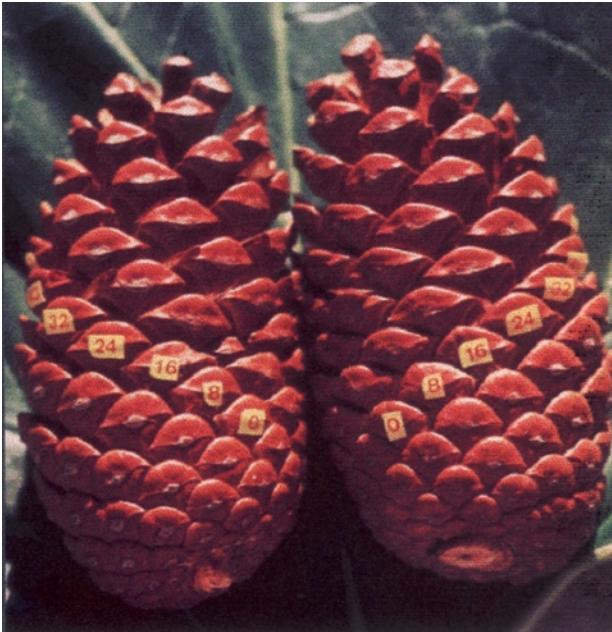


Figure 7 All spiral phyllotaxes show chirality. For example, there are as many right-handed as left-handed pine-cones on a tree (*Pinus* sp.). The 8 contact parastichies can run from bottom right to top left or from bottom left to top right.

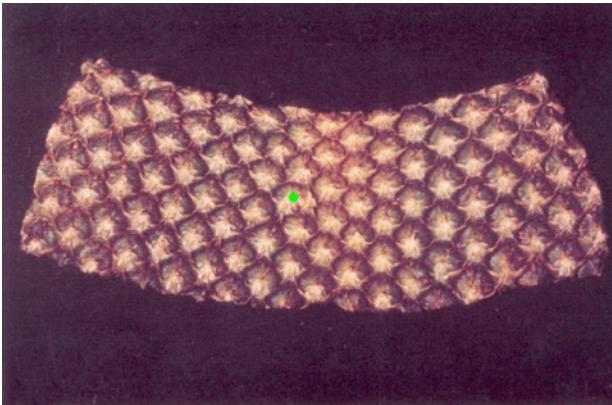


Figure 8 Surface of an aberrant pineapple (*Ananas comosus*), peeled off and unrolled. There are eight parastichies running from bottom left to top right. Two of the 12 parastichies running from bottom right to top left fuse into one (green dot); thus there are only 11 parastichies higher up. Normal pineapples show contact parastichy patterns of [8 + 13].

Parameters for Quantitative Phyllotactic Analysis

Divergence angle d

This is the smaller of the two angles at the centre of a rosette or a transverse section of a shoot tip determined by consecutively initiated leaves along the genetic spiral

(**Figure 4**). Defined ranges of divergence angles characterize the various types of spiral systems (e.g. Lucas systems with $d \approx 99.5^\circ$; **Figure 3**).

Leaf arc = leaf insertion angle i

This is the insertion angle of leaf primordia. Except for the Fibonacci systems, which are quite variable with respect to the leaf arc ($\sim 40^\circ < i < 360^\circ$), many phyllotactic systems have more or less clearly defined leaf arcs (e.g. Lucas systems with $i \approx 60^\circ$).

Plastochron ratio R

This ratio equals the ratio of the distances of two successive leaf primordia from the centre of the SAM. It is denoted by $R > 1$ and is a measure of the relative radial distances of the young leaves in the bud as compared to the relative size of the SAM. It is probably a consequence of optimal packing that radial distances of young leaves increase with a nearly constant ratio (i.e. exponentially) within a tightly packed bud. Thus, parastichies are often logarithmic spirals or nearly so when seen in cross-sections of shoot tips (buds) with densely packed leaves (as simulated in **Figure 9**) Various phyllotactic patterns can be characterized by certain ranges of R (see Jean and Barabé, 1998)

Contact parastichy numbers k

In regular spiral patterns with densely packed leaves the contact parastichies are the curved lines along which leaves (or florets in sunflower and pineapple) have contact with each other. In typical Fibonacci patterns there may be a set

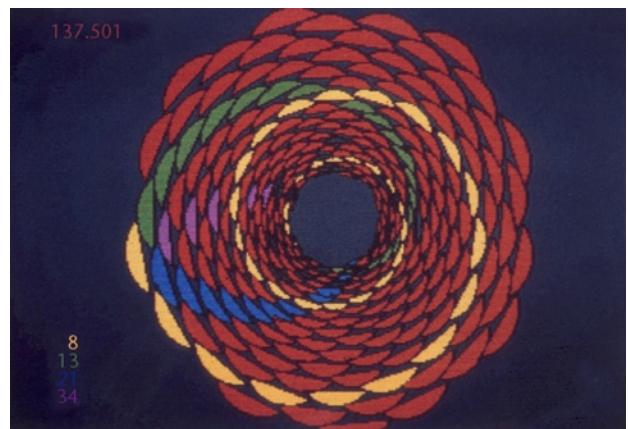


Figure 9 Computer-simulated Fibonacci system illustrating cross-section of shoot tip with tightly packed leaves. One sample of each recognizable parastichy set is marked with a different colour: 13 (green) and 21 (blue) are the most conspicuous contact parastichy sets. Less obvious are parastichy sets along which the leaves have (nearly) no contact: 8 (yellow) and 34 (pink).

of 13 right-handed (clockwise) contact parastichies and a set of 21 left-handed parastichies (Figure 9). Shoot tips with broader leaf bases (i.e. higher i values) and bigger leaf primordia as compared to SAM size (i.e. higher R values) show lower k numbers such as '5' and '8' in Fibonacci systems.

Using plastochron ratio and leaf arc as quantitative parameters for the relative size of the leaf primordia as compared to the SAM, phyllotaxy becomes a continuously varying function. The plastochron ratio of many seed plants decreases from the seedling stage to the established shoot and further to the flowering stage. Correlated with this are decrease in leaf arc, increase in contact parastichy numbers (e.g. higher elements of the Fibonacci sequence in spiral systems), acceleration of leaf inception, and sometimes a change of phyllotaxy patterns, e.g. from decussate to spiral systems.

Definition and Fuzziness of Phyllotactic Patterns

The diversity of regular phyllotaxy patterns in vascular plants is summarized by various contributors in Jean and Barabé (1998) (see Further Reading). The mathematical beauty of various phyllotactic patterns has been shown by Prusinkiewicz and Lindenmayer and by van der Linden using computer simulations.

Distichous (including spirodistichous) patterns (with $150^\circ \leq d \leq 180^\circ$)

Such patterns are found in many monocots and some dicots (e.g. Apiaceae, Ranunculaceae) with leaves enveloping the stem (node) considerably or totally, i.e. with leaf arcs $220^\circ \leq i \leq 360^\circ$. This coincides with experimental data from maize (*Zea mays*). Accumulation patterns of *terminal ear 1 (te1)* transcripts in SAMs of maize are horseshoe-shaped, giving a prepattern according to which a leaf with a broad sheathing leaf base is formed. A new leaf primordium in maize is then initiated in the SAM region corresponding to the open end of the horseshoe, where no *te1* transcript is detected.

Spiral patterns, especially Fibonacci and related patterns

The most common spiral phyllotactic patterns are called Fibonacci patterns. They show divergence angles approaching 137.5° and contact parastichy numbers according to the Fibonacci sequence 1, 2, 3, 5, 8, 13, 21, 34, 55, ... Less frequent are accessory spiral patterns that are correlated with narrow leaf bases (insertion angles $i \leq 60^\circ$) and low plastochron ratios ($R < 1.2$). Most

notable among them are the Lucas systems (Figures 3 and 5) with divergence angles $d \approx 99.5^\circ$ and contact parastichy numbers according to the sequence 1, 3, 4, 7, 11, 18, 29, 47, ... Again closely related to the typical Fibonacci patterns are the bijugate systems, which are also called double Fibonacci patterns (Figure 6). These consist of consecutive leaf pairs that are twisted $\sim 68.8^\circ$ (i.e. half Fibonacci angle). Their contact parastichy numbers correspond to the series 2, 4, 6, 10, 16, ... (i.e. double Fibonacci numbers). Fibonacci, Lucas and bijugate systems are observable in the same species, for example in sunflower capitula and pine cones.

Decussate phyllotaxy = decussation

This is another frequent phyllotaxy among seed plants. There is simultaneous initiation of two opposite leaves while the next leaf is alternate, i.e. turned 90° (Figure 1). Nearly all dicots start seedling growth with decussation: one pair of cotyledons followed by at least one pair of plumular leaves. Decussate systems consist of leaf pairs, i.e. dimerous whorls, and thus may be viewed as a case of whorled systems (see below). There are spirodecussate systems (e.g. in *Sagina*, Caryophyllaceae) that can be seen as intermediate between typical decussation and spiral Fibonacci systems.

Whorled systems

Whorls are ring-like arrangements of leaves (or scales, bracts, floral organs) along an axis. The members of a typical whorl are initiated simultaneously (Figure 2). Successive whorls normally arise acropetally at the SAM, show an equal number of leaves, and alternate with each other. Thus, the leaves belonging to the first, third, ... whorls contact each other along straight lines (orthostichies) that are alternate to the orthostichies connecting the leaves of the second, fourth, ... whorls. Members of the same whorl may form a tube due to interprimordial growth or common girdling primordium. Whorled and spiral phyllotaxy, however, are overlapping categories, with spirally distorted whorls as an intermediate condition (Figure 8). The leaf whorls of *Lycopodium sensu lato* and *Peperomia* show both simultaneous and spiral inception of the whorl subunits, depending on the species. Both simultaneous and spiral initiation are found in floral whorls. Whorled sepals often arise along a $2/5$ spiral reflecting a Fibonacci pattern.

Hofmeister's rule and exceptions

Hofmeister postulated in 1868 that new leaves arise on the SAMs in those positions that are as far as possible from the insertion area of the nearest existing leaf primordia. This rule is known as Hofmeister's rule: new leaves always arise

in the largest gap between existing primordia as observable in most phyllotactic patterns. Exceptions to Hofmeister's rule do exist, however. (1) Superposed whorls occur in many flowers with respect to stamen positioning as compared to the perianth. For example, flowers of Primulaceae have five stamens that occupy exactly the sectors of the petals. Superposition = sectorial cohesiveness of stamens and perianth members may be explained by McConnell and Barton's cyclic model for shoot development (i.e. similar to axillary branching). (2) Superposed whorls also occur outside the floral region. The bladderwort *Utricularia purpurea* has stems with superposed whorls that are normally pentamerous. (3) Monostichy, the alignment of all leaves along a single sector (orthostichy), is found in various ferns and a few flowering plants such as *Utricularia sandersonii*. (4) Spiromonostichy is a rare phyllotaxy that is found in Costaceae, although the related ginger (Zingiberaceae) show distichy and thus obey Hofmeister's rule. In all members of Costaceae consecutive foliage leaves along the genetic spiral normally show very low divergence angles ($50^\circ < d < 90^\circ$) resembling winding stairs.

Irregular phyllotaxy

This term indicates leaf inception without an obvious regular pattern. Other terms for irregular phyllotaxy have been used – chaotic, erratic, perturbed or random phyllotaxy. Irregular patterns can show acropetal or basipetal organ inception or no preferred direction at all (e.g. in *Acacia* spp.). Irregular phyllotactic patterns are also observable in flowers with polystemony, such as *Exospermum* (Winteraceae) and *Phytelephas* (Arecaceae). As a result of mutations that change the shape of the SAM considerably (e.g. crest-like SAM shape in fasciation mutants), the usual Fibonacci phyllotaxy in *Arabidopsis* is replaced by an irregular one. The *fev* (for ever young) mutant results in a disruption of leaf positioning and meristem maintenance. Almost half of the *fev* leaf primordia are centric, that is lacking dorsoventral symmetry. In the sunflower capitulum the florets are irregularly incepted after wounding and other treatments. For altered phyllotaxy after experimental interference in other plants see Meinhardt *et al.* in Jean and Barabé (1998).

Phyllotaxy Theories

There are several developmental hypotheses explaining the patterning of primordia around SAMs. Crucial to understanding how leaf phyllotaxy is controlled as a physiological process is the question of how information is communicated among the cells of the SAM, so that cells at particular sites can be targeted to change their polarity, as the first step in the production of a leaf primordium.

There is no generally accepted physiological theory of phyllotaxy backed by experimental evidence. Three major hypotheses are as follows. (1) The inhibition field theory is mainly based on the diffusion of morphogens in SAMs. These endogenous gradients may lead to local exclusion (lateral inhibition) of leaf inception, whereas they may promote long-range induction of new leaves. (2) According to the biophysical theory of undulating fields, cortical microtubules and cell wall cellulose microfibrils are reoriented in the SAM where and when a new leaf primordium is formed. There is experimental evidence that endogenous cell-wall loosening proteins (called expansins) are involved in cellulose microfibril reorientation. The induction of leaves and leaf-like organs, then, is effected via altered biophysical stress patterns. (3) According to the French school (e.g. Cottignies), phyllotaxy patterns are the result of partitioning activity of spirally arranged leaf-forming zones around the SAM. Along these formative helices a leaf primordium gives rise to a new one by homeogenetic induction. New experimental evidence has been proposed also in favour of this French school view. The three phyllotaxy theories are complementary rather than contradictory views. They assume that new leaf sites are established by hypothetical diffusing chemical fields of growth promoters or growth inhibitors, originating from both the SAM and the youngest leaf primordia.

Molecular developmental genetics versus biophysics

The variety of phyllotactic patterns possible within a plant or along a single shoot stresses the importance of biophysical factors controlling phyllotaxy. Some patterns (e.g. Fibonacci phyllotaxy) optimize dense packing of leaf primordia in shoot buds. According to molecular developmental genetics, the positioning of leaf primordia at the SAM is correlated with (and thus may depend on) the downregulation of *knotted-1 like* homeobox genes. However, it seems that several phyllotactic patterns are not directly encoded in the genes. Regular phyllotactic patterns are to a considerable degree the result of physical self-organized growth processes within the SAMs as shown by Douady and Couder.

Adaptive value of phyllotactic patterns

Fitness landscapes for vertical shoots with different phyllotactic patterns have been proposed by Niklas. The occurrence of an astonishing diversity of phyllotaxy patterns in a single species or even an individual (e.g. *Abies*, *Picea*, *Magnolia*), however, points to a considerable degree of nonadaptiveness of morphological variation with respect to phyllotactic patterns.

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