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INVITED REVIEW

The riddle of phyllotaxis: exquisite control of divergence angle

Takuya Okabe*

Graduate School of Integrated Science and Technology, Shizuoka University, Hamamatsu 432-8561, Japan

* Email: okabe.takuya@shizuoka.ac.jp

Abstract

Phyllotaxis studies published in German in the 1930s have reported intriguing regularity in the arrangement of incipient leaves on shoot apices of a wide variety of plant species. However, these studies have received little attention today, even though they provide a crucial evidence base for understanding this mathematical phenomena. Here I recapitulate the essential point by means of illustrative examples. It is emphasized that accurate control of apical divergence angle is at the heart of the numerical riddle of spiral phyllotaxis. The accurate patterning at the shoot apex has an unexpected evolutionary benefit of being optimally adaptive in the subsequent events of phyllotactic change to occur on an elongating shoot.

Keywords

golden angle; Fibonacci numbers; evolution by natural selection; optimality; Schimper–Braun; Max Hirmer

Introduction

Fibonacci numbers 1, 2, 3, 5, 8, 13, 21, 34, etc., manifested in the disposition of various organs of higher plants have been a long-standing source of wonder. Most notably, these numbers are found by counting curved rows of seeds on a sunflower head. A curved spiral connecting contiguous organs is called a contact parastichy. Although this observation attracts people's attention first and foremost, the aim of this paper is to show that the occurrence of Fibonacci numbers in contact parastichies is nothing but the tip of the iceberg of the truly intriguing phenomena of phyllotaxis. More often than not, the phyllotaxis literature in the nineteenth century has expressed the arrangement of adult leaves on a stem by means of a Schimper–Braun fraction like $1/2$, $1/3$, $2/5$, $3/8$, $5/13$, $8/21$, etc., which signifies the angle of divergence between consecutive leaves expressed in terms of a fraction of a full turn. If the divergence angle is expressed in degrees, they represent 180° , 120° , 144° , 135° , 138.46° , 137.14° , etc., respectively. Around the turn of the twentieth century, the research interest was shifted to the arrangement of leaf primordia on the shoot apex. By the 1930s, it was recognized and established gradually and presumably independently that, instead of Schimper–Braun fractions, divergence angles of leaf primordia are fixed at a constant value intriguingly close to the mathematical limit of the above sequence, that is, 137.508° (Fig. 1) [1–4]. In concert with rising interest in the apical arrangement, the phyllotaxis fraction gradually dropped out of the main stage of science. Fig. 2 is an abridged chronology of phyllotaxis studies during this period and thereafter.

In the next section, I begin with reviewing German studies in the 1930s (Fig. 2). Today these studies are neglected almost entirely. For example, the most comprehensive monograph of 386 pages with 898 references by Jean [5] makes no reference to this series of studies [6–11]. In view of this situation, I come to realize that most researchers are unaware that theoretical models including modern variants have

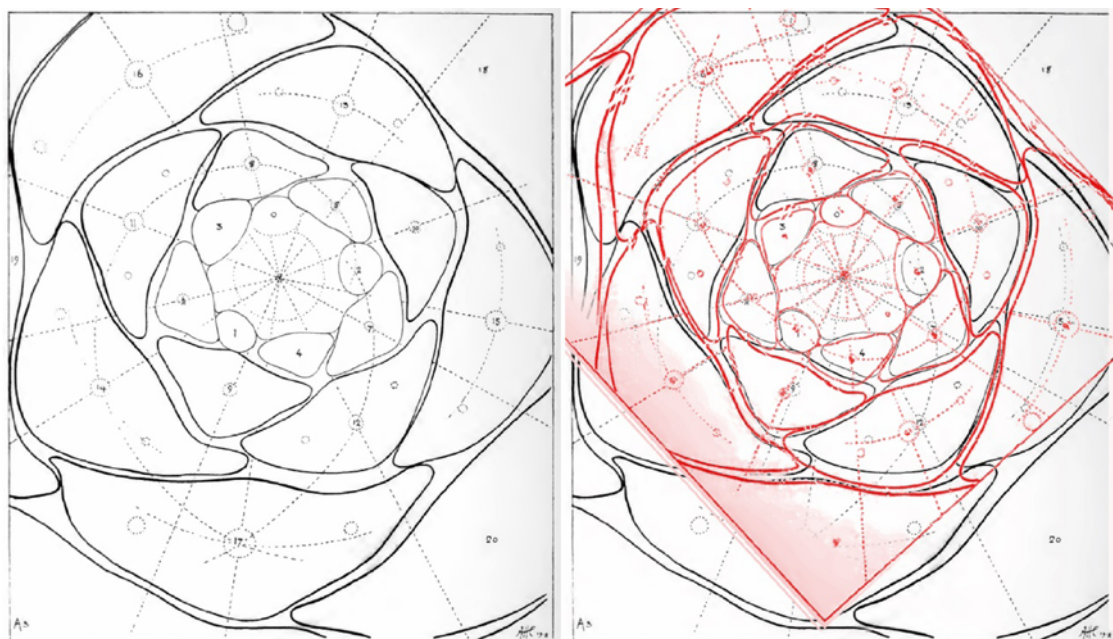


Fig. 1 (Left) A shoot apex of *Sempervivum calcaratum*, showing fairly constant divergence angles of $137 \pm 1^\circ$. Measured angles are tabulated in p. 28 of Church [2]. (Right) A contracted image rotated by 137.5° (in red) is overlapped on the original figure (left). Adapted after Fig. XII of Church [2] (not copyrighted).

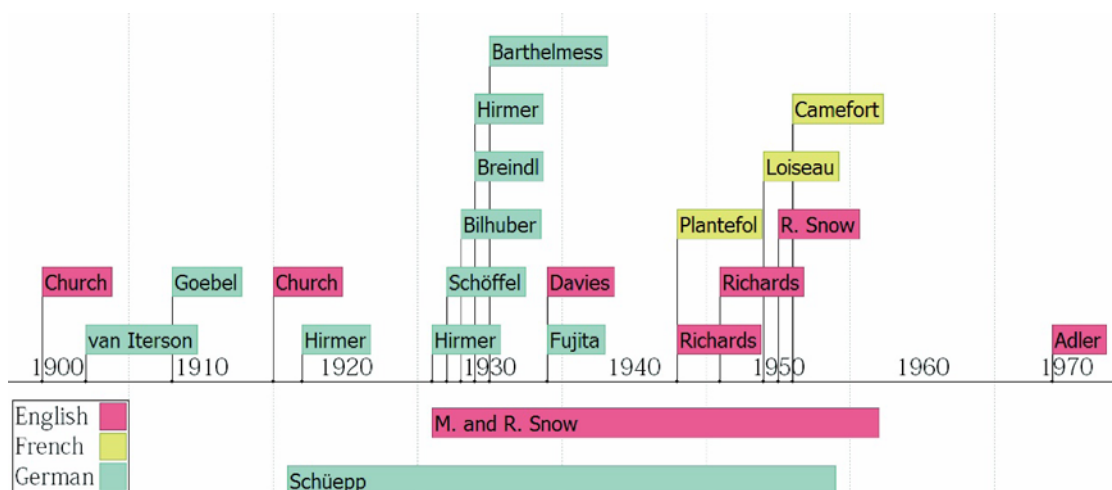


Fig. 2 An abridged chronology of phyllotaxis studies arbitrarily compiled from a theoretical perspective.

difficulties related to these neglected observations [12–18]. In the section titled “Acceptance of the ideal angles”, I follow the study history of F. J. Richards and Robert and Mary Snow, the early British researchers most influential to this day, and argue that the neglect is caused by historical contingency and intellectual inertia. Here I call attention to the overlooked fact that the Snows did not recognize difficulties of a space-filling theory until their late years [12,13]. The penultimate section “Evolutionary explanation” gives a brief account of a “hidden” adaptive significance of the ideal angle 137.5° . The presented view brings back to light the long-neglected observations of Schimper and Braun. As this theory is based on the established facts of what happens on elongating shoots, it claims that the incipient angle 137.5° cannot be understood just by investigating what happens at the shoot apex. The reader should be reminded in advance that an evolutionary perspective in general has been disregarded almost completely in phyllotaxis, although it has not been explicitly rejected [1]. The generally accepted wisdom is that phyllotaxis is the emergence of order through non-adaptive mechanics of developmental processes [12–18], while the Snows leave room for the act of natural selection as a last resort [12,14]. The relevance of non-adaptive

mechanisms is supported by the observation that an individual plant occasionally shows different phyllotactic patterns [19]. Diversity in phyllotaxis is a subject of great interest [20,21]. The frequency of occurrence of different types of patterns may have little to do with natural selection [22,23]. However, regularity and diversity in phyllotaxis are different issues. Indeed, the lack of regularity may be a cause of diversity whereas the lack of diversity does not imply regularity. The presence of regularity in vivo requires a special explanation of its own. The concluding section mentions the Bravais brothers, who are the original proponents of the universal constancy of incipient divergence angle [24].

The scope of this paper is limited to the regularity in spiral phyllotaxis, especially to its mathematical exactitude. This aspect has not been duly appreciated for the good reason that mathematical finesse is not a rule in empirical sciences. All experimental measurements have some uncertainty. The four digit number 137.5 for a measured angle implies an uncertainty of about 0.1, i.e., $137.5 \pm 0.1^\circ$. In a quantitative science, to which phyllotaxis belongs, the error 0.1 carries no less important information than the mean itself. Indeed, the error represents a quantitative measure of regularity. The more accurately the special number 137.5 is realized in nature, the larger Fibonacci number manifests itself in a non-trivial manner. Therefore, the use of a vague expression like “about 137.5” leads to an underestimation of the point at issue. Empirical as well as mathematical studies in which accuracy does not matter fall outside the scope. As seen below, the actual accuracy in incipient divergence angle appears so high that the true nature of the problem is appreciated only at the level of an organ system, but not fully at the level of meristematic cells. Accordingly, the present subject matter is remotely related to the recent advances in plant development [25,26]. Still it may be worthwhile to note here how phyllotaxis theorists consider the role of genes. Although whether the ideal angle is adaptive or not is difficult to determine experimentally, it has important implications for the hypothetical role of genes. An adaptive (or Darwinian) view comes to terms with the assumption that the angle is determined and controlled by genes. Non-adaptive (non Darwinian) mechanisms are categorized into two groups, depending on whether it rests on gene instructions or not. Unfortunately, this point has not been appreciated because the conceptual divide between the two groups is so deeply rooted in a cultural divide between researchers with different backgrounds that their respective views on genes are often not stated expressly. Generally speaking, biological scientists do not doubt the central role of genes [12–14], while physical scientists downplay the importance of gene instructions [15–18]. Thus, the mechanisms are classified into three categories: genetic adaptive, genetic non-adaptive, and non-genetic. The enlightening physics experiment by Douady and Couder [12] spurred the recent surge of interest in models of the last category. Therefore, it is of utmost importance to understand whether and to what extent the phyllotactic pattern is controlled by genetic (heritable) factors. The basic question is in what sense the apparently fixed value of incipient divergence angle is stable. A key would be provided if the fixed value is experimentally manipulated without losing the stability.

German literature in the 1930s

In 1922, Hirmer categorized phyllotaxis patterns into two types (simple and duplicated) and each further into two (regular and not regular). He argued that all spiral systems belonging to the last category have one and only divergence angle, namely, 137.5° or 99.5° , depending on the number of system components. The fundamental significance of the unique divergence angle is underscored in the subsequent paper published in 1931 [6]. As illustrated in Fig. 3, the organs hypothetically arranged at constant intervals of 137.5° make two different sizes of gaps (wide and narrow) if the number of the organs equals Fibonacci numbers 2, 3, 5, 8, 13 (framed in Fig. 3). Otherwise, three sizes of gaps occur (not framed in Fig. 3). Hirmer remarks that ray florets and involucre bracts of asters are arranged in conformity with this theoretical arrangement (Fig. 4). They are known to occur preferentially in Fibonacci numbers [27,28]. Hirmer explains this tendency based on the availability of space and substance to

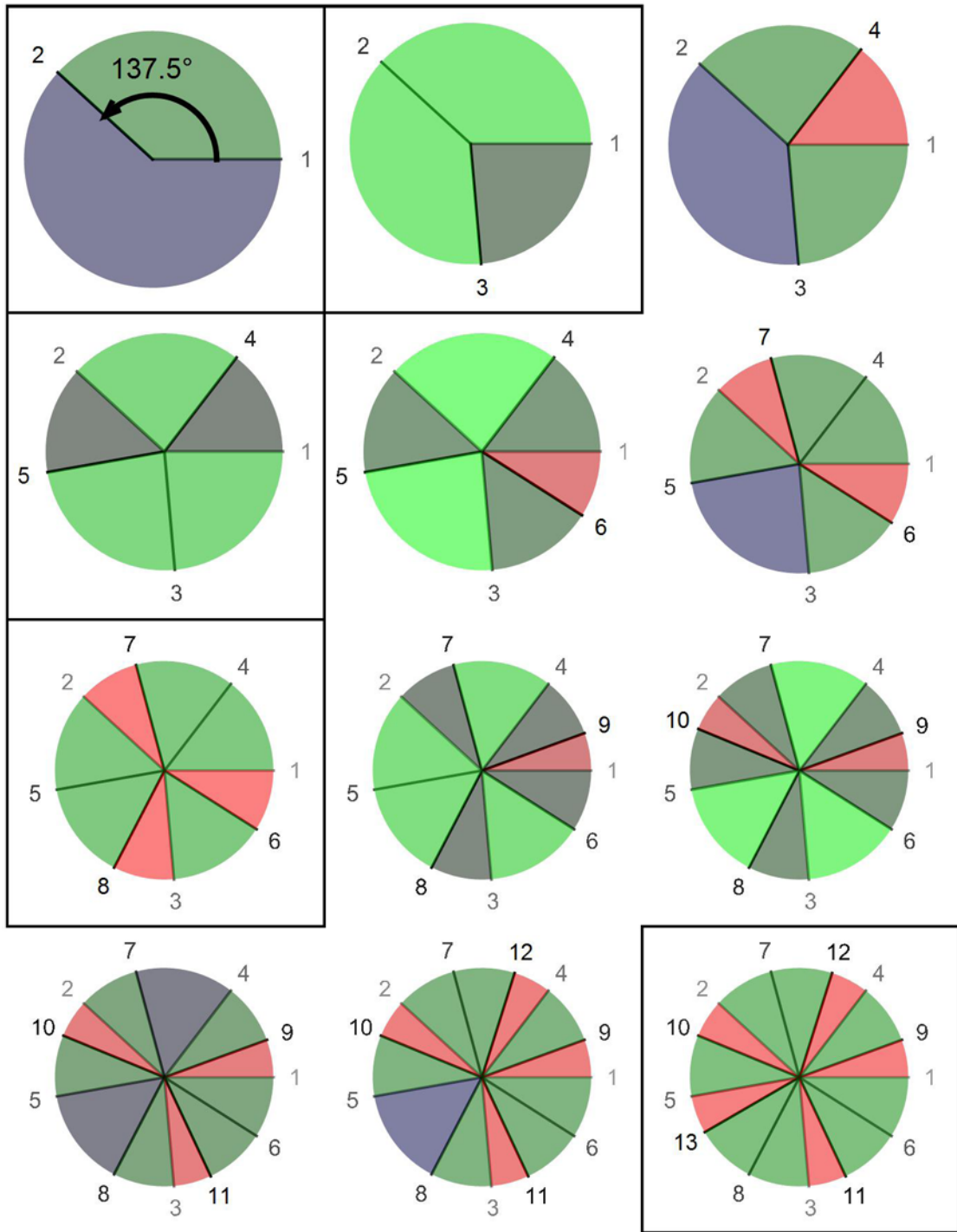


Fig. 3 Theoretical arrangement of organs placed at constant angular intervals of 137.5° . Each panel has a different number of organs. Gaps of different sizes are indicated with different colors. There are two different sizes of gaps when the total number of organs agrees with a Fibonacci number, i.e., 2, 3, 5, 8, and 13 (framed). Otherwise, there occur three sizes of gaps (not framed). It is the mathematical consequence of this angle (137.5°) that the latest organ always occurs such as to divide the oldest of the largest existing gaps with the golden ratio 1:1.618. Note also that the difference in numbers (ages) of adjacent organs is without exception a Fibonacci number. Thus, the angle 137.5° is the cause of Fibonacci numbers in contact parastichies.

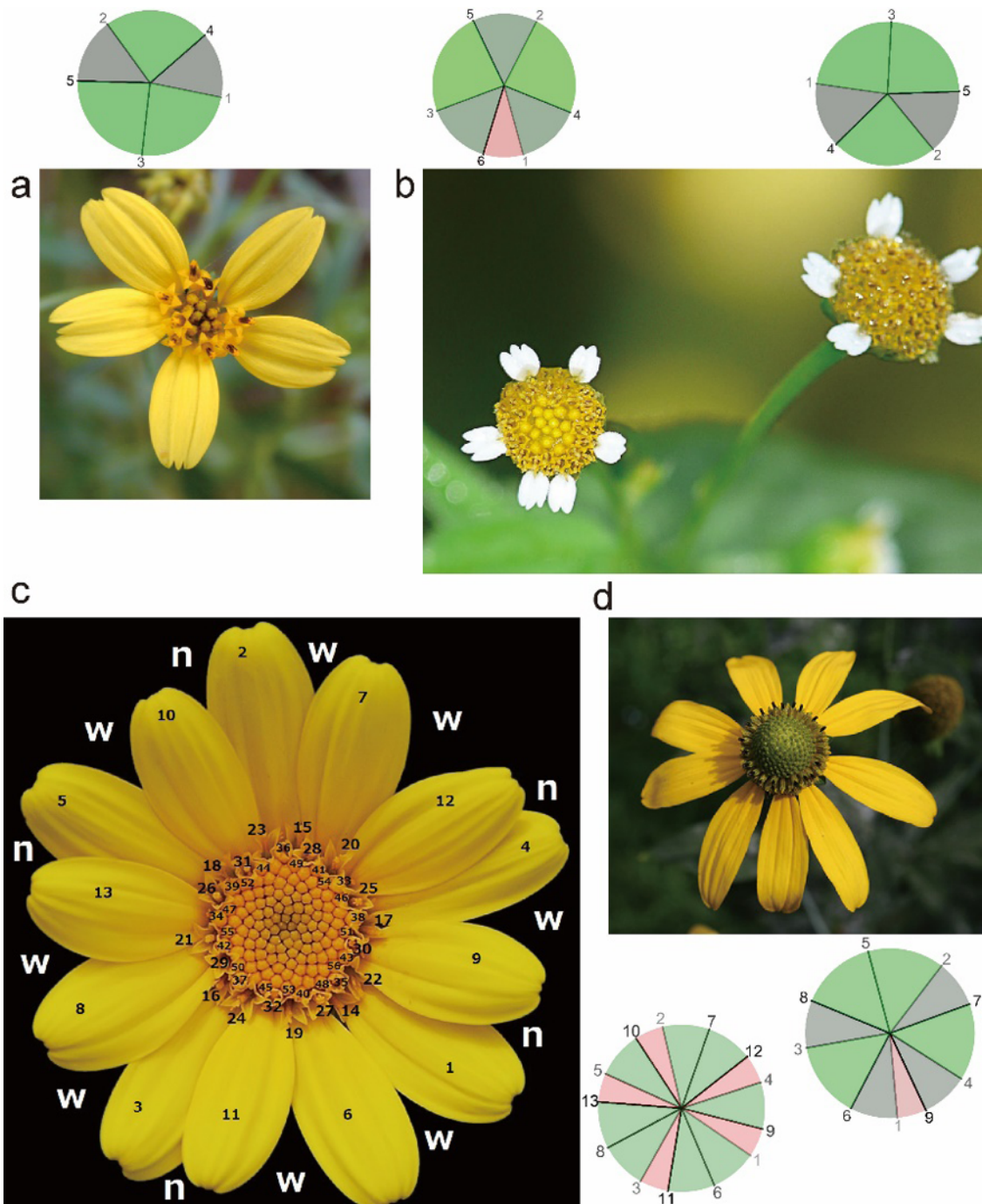


Fig. 4 Petal arrangement in accordance with the 137.5° arrangement. For comparison, theoretical arrangements are shown next to respective flower images. **a** *Bidens torta* (CC BY-SA 3.0) [63]. **b** *Galinsoga parviflora* (CC BY-SA 3.0) [64]. **c** *Anthemis tinctoria*, adapted (CC BY-SA 3.0) [65]. Counterclockwise from Petal 1 (bottom right), wide and narrow gaps (denoted as “w” and “n”) are arranged in conformity with the 137.5° arrangement. i.e., n (red), w (green), n, w, w, n, w, n, w, w, n, w, and w. **d** *Rudbeckia laciniata* (CC BY-SA 3.0) [66].

induce floral organs. If the number of organs is not a Fibonacci number, there occurs a gap or gaps of a third size, which are liable to intake inducing substances until the organ number matches a Fibonacci number. Furthermore, it is noted that the 137.5° arrangement persists even when ray florets are distributed asymmetrically in a lop-sided manner. Thus, the appearance of Fibonacci numbers is nothing but a secondary consequence of the prevailing rule of the constant divergence angle 137.5° . Hirmer maintains that it is a fundamental mistake to give significance to contact parastichy numbers, for they are only the expression for the relation between the relative size of the vegetation point and organ primordia [6: p. 137]. Subsequently, Schöffel shows that distinctive flower patterns of various genus in Ranunculaceae provide especially clear evidence for this view. Whether radial or dorsiventral, incipient organs in spiral phyllotaxis are arranged at constant angles of 137.5° or rarely 99.5° [7]. Even in succulent plants, Bilhuber provides further support that organs at the shoot apex of a large number of species in Cactaceae and Euphorbiaceae are most frequently arranged according to the angle 137.5° . In addition, other ideal divergence angles 99.5° , 78.0° , and 64.1° as well as bijugate and trijugate patterns by a half and a third of these angles are found [8]. Breindl shows that the spiral arrangement of floral parts of dicotyledons is under the structural influence of the 137.5° divergence angle [9]. He discusses deviations from the ideal arrangement on a case-by-case basis. The patterns of calyces of many dicotyledons are intermediate between the 137.5° arrangement (with unequal spacing) and a regular-polygonal arrangement (with equal spacing) [9]. Barthelmess confirms the 137.5° angle on the growing point of Coniferae. By means of more than a thousand individual measurements, he showed that the 137.5° angle is predominant in the patterns of vascular bundles not only as the mean value of a statistical distribution but as the peak in the frequency of occurrence [10]. These advances are reviewed by Hirmer [11]. Then, Fujita reports the presence of a new angle 151.1° on the shoot apex of *Cephalotaxus drupacea* as the peak value of the statistical distribution curve of measured divergence angles [29]. In a more comprehensive analysis, Fujita presents distribution curves of divergence angles as observed in transverse sections of shoot apices of 30 species of flowering plants, which are reproduced in Fig. 5 [30]. Fujita's results are a synthesis of the preceding studies rather than a new discovery. Indeed, Barthelmess [10] and Davies [31] reported similar curves of cumulative results for mature shoots of *Podocarpus chinensis* and for four stages of *Ailanthus altissima*, respectively.

Even without knowing the above development, the significance of the 137.5° angle is noticed on a close inspection of photo images of good quality. If divergence angles are directly measured from digitized images, they will show more or less fluctuations to a degree consistent with the prior results (Fig. 5). As a matter of fact, the statistical fluctuations are not random [32–34] but they are correlated as if the pattern as a whole is deformed by physical effects of mechanical stress [35]. As shown in Fig. 6, a collective deformation disturbs individual divergence angles. The correlated fluctuations due to a local disturbance cancel out on average. Accordingly, the statistical significance of the ideal angle 137.5° is readily confirmed by averaging divergence angles of several consecutive leaves. In short, the fluctuations are not intrinsic to the plant. Another method for confirming the relevance of the ideal angle is provided by inspecting positional correlation of distant leaves. This is not always feasible not only because of secondary shifts in position of growing leaves but because of a pattern size limitation. The left of Fig. 7 shows an ideal arrangement after the constant angle 137.5° . In the ideal arrangement, leaves of (plastochron) ages differing in Fibonacci numbers, 1, 2, 3, 5, 8, 13, 21, 55, 89, etc., tend to approach a radial line through the center. However, if the constant angle deviates from the ideal value 137.5° , these leaves deviate from the radial line, as shown in the right of Fig. 7. Therefore, even a slight deviation from the ideal angle 137.5° may be judged from how Fibonacci numbers are arranged in the pattern. To find a large Fibonacci number, it is convenient to use a mathematical formula, $G_{n+1}F_{m+1} + G_nF_m = G_{n+m+1}$, where (G_{n+1}, G_n) and (F_{m+1}, F_m) are pairs of consecutive Fibonacci numbers. For example, a large Fibonacci number 89 is obtained from Fibonacci-number pairs (21,13) and (3,2) as $21 \times 3 + 13 \times 2 = 89$. This equation has a graphical interpretation, as indicated with arrows in Fig. 7. Starting from 0 (bottom of Fig. 7), three steps along a 21 parastichy plus two steps along a 13 parastichy lead to 89. Fig. 8 shows conifer cones of *Picea abies* by Braun [36], in which scales differing by

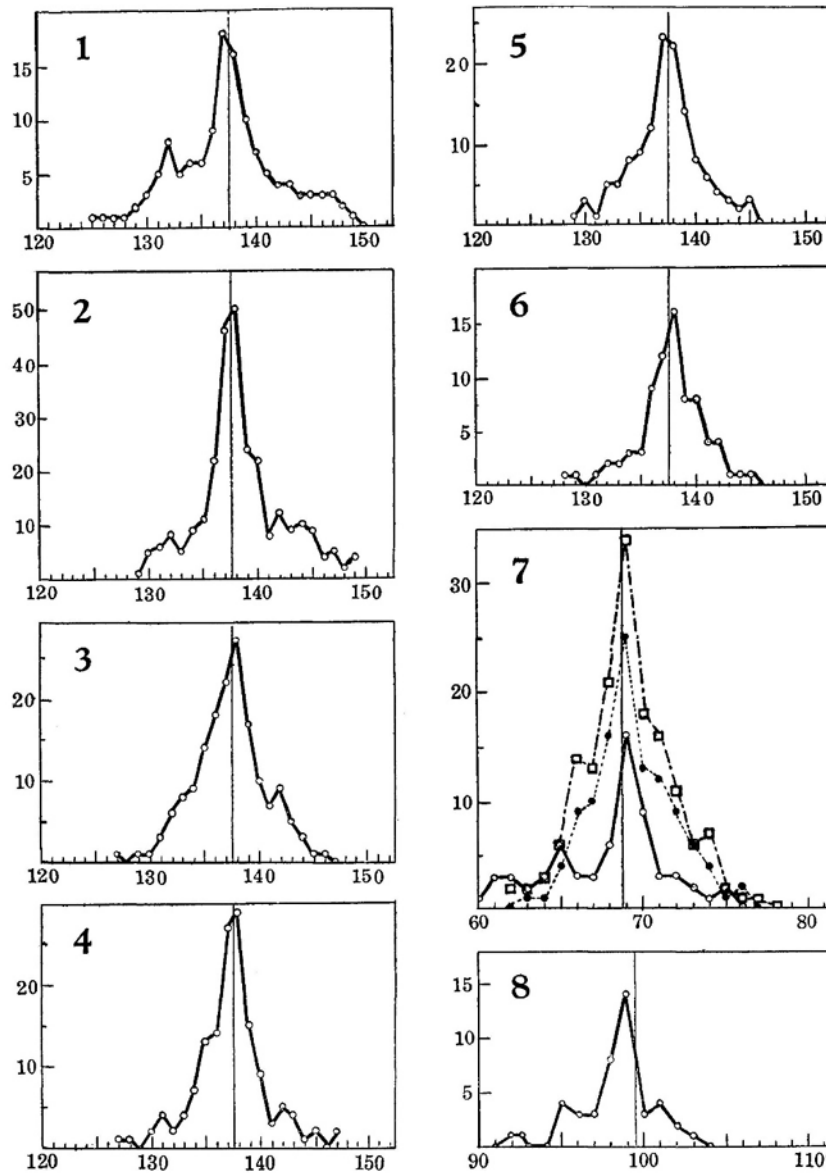


Fig. 1-8. Variationskurve der Divergenz bei den Schraubenstellungen mit verschiedenen konjugierten Parastichen.

- (1) *Lysimachia clethroides* 1:2, (2) *Lycium chinense* 2:3, (3) *Lobelia sessilifolia* 3:5,
 (4) *Cephalotaxus drupacea* 5:8, (5) *Senecio vulgaris* 8:13, (6) *Eclipta alba* 13:21,
 (7) *Cephalotaxus drupacea* ○—○ 2:4, ●—● 4:6, □—□ 6:10,
 (8) *Cunninghamia lanceolata* 4:7.

Fig. 5 Frequency distribution curves of divergence angles in spiral arrangements with various parastichy pairs. Reproduced from Fujita [30] with permission from the Botanical Society of Japan.

Fibonacci numbers are indicated with circles. According to Braun, all but 3% of more than a thousand cones of this species show the normal arrangement 8/21, 13/34, and 21/55, while he remarked a single rare variant 18/47, namely 137.87°. Braun recorded this exceptional pattern as a drawing, which is reproduced in the center of Fig. 8. This pattern shows a sign of deviation from ideality. Note that all patterns in Fig. 8 are classified as the normal pattern 5:8 in terms of contact parastichies. The minute differences of current interest are not discernible without using multi-digit numbers for divergence angle. Indeed, errors of various origins make it generally difficult to reject the null hypothesis that the mean of measured angles coincides with the exact value of the golden angle $180(3 - \sqrt{5}) \cong 137.508$. Fig. 9 shows a capitula of *Helianthus annuus* indicating a slight but statistically significant deviation from the exact value, namely $137.513 \pm 0.003^\circ$ [37]. Fig. 10 shows a shoot apex of *Sequoia sempervirens*,

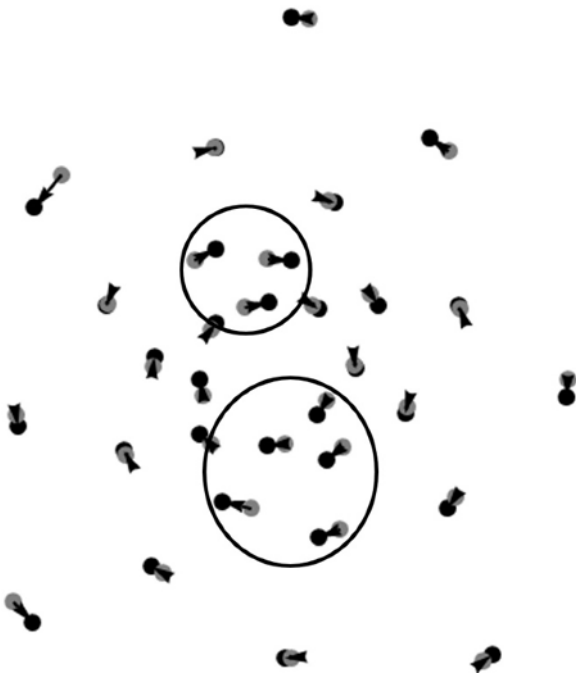


Fig. 6 Arrows indicate displacement of leaf positions (black dots) from the ideal arrangement by 137.5° (gray dots). Collective shifts as indicated in circles cause correlated fluctuations in the raw values of divergence angle. However, these shifts do not affect the mean value 137.5° . Accordingly, the natural occurrence of the angle 137.5° is immediately confirmed by averaging divergence angles of several consecutive leaves (i.e., of several turns around the stem) [35]. This observation indicates that the angle 137.5° is intrinsic to the plant and the apparent fluctuations are not of fundamental significance.

which indicates positional correlation between distant leaves n and $n+21$ ($n = 0, 1, 2, 3, \dots$). As indicated by numbers in the circumference of Fig. 10, leaves are arranged clockwise in the order 1, 14, 27, 6, 19, 32, 11, 24, 3, 16, 29, 8, and so on. This is just as expected from the ideal angle 137.5° . The bottom-right end of Fig. 3 indicates the same order 1, 6, 11, 3, 8, and so on. These results indicate that the ideal angle 137.5° is maintained surprisingly accurately. Fig. 11 illustrates subtlety of a one-degree accuracy of divergence angle.

Interestingly enough, the same order is found in tentacles of hydrozoan jellyfishes (Fig. 12) [38,39]. The spiral direction in jellyfish is not random as in plants. However, the overall processes of growth and formation of lateral organs in jellyfish medusae are comparable to those of flowering plants [40: p. 420–423]. According to a mathematical theorem, when organs are successively placed at constant angular intervals, gaps formed by the organs have at most three different sizes. Moreover, the next organ always arises in (the oldest of) the largest existing gap(s) (Fig. 3). These properties hold true for any value of the constant angle. The uniqueness of 137.5° is in that this angle gives the “most uniform” distribution in the sense that the organs are kept away from each other most effectively [39,41,42].

Acceptance of the idea of the ideal angles

According to a literature search in English publications, it is not until 1955 that the 1931 paper of Hirmer [6] is cited by Robert Snow [12]. Then follow Puławska [43], Kumazawa and Kumazawa (1971) [32], Endress (1980) [44], Kubitzki (1987) [45], Endress (1990) [46], Bachmann et al. (1993) [34,47,48], Barabé (1995) [49], and so forth. An important

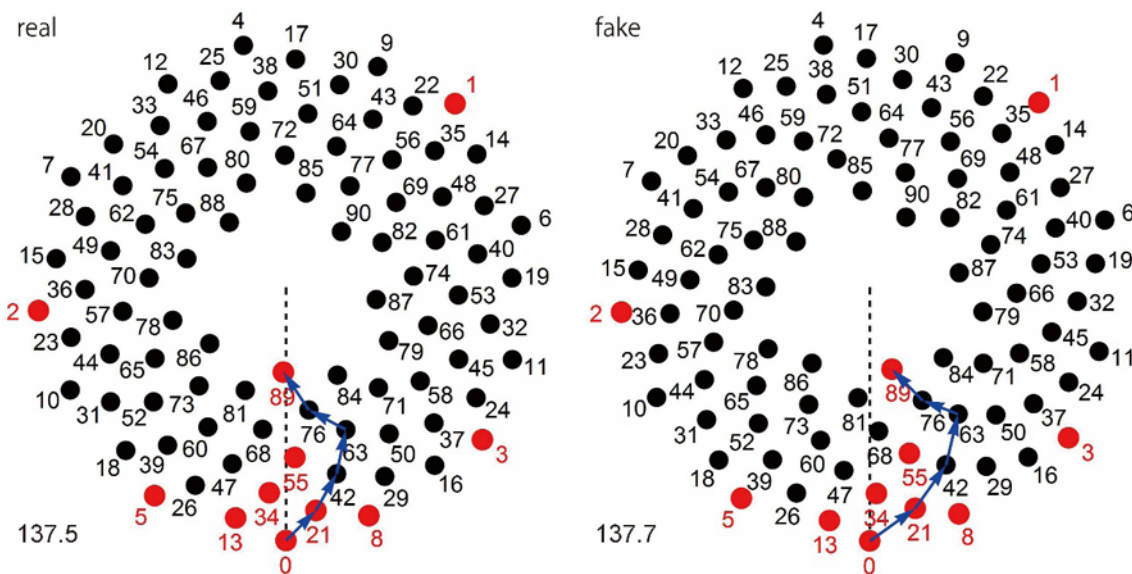


Fig. 7 Regular arrangements with the ideal angle 137.5° (left) and a slightly different angle 137.7° (right). In the ideal case (left), Fibonacci numbers (in red) converge to a radial line through 0 (dashed). A path of arrows indicates a graphical illustration of the equation $21 \times 3 + 13 \times 2 = 89$. The right pattern (137.7°) is very unlikely to be found in real sunflowers (cf. Fig. 9) [37].

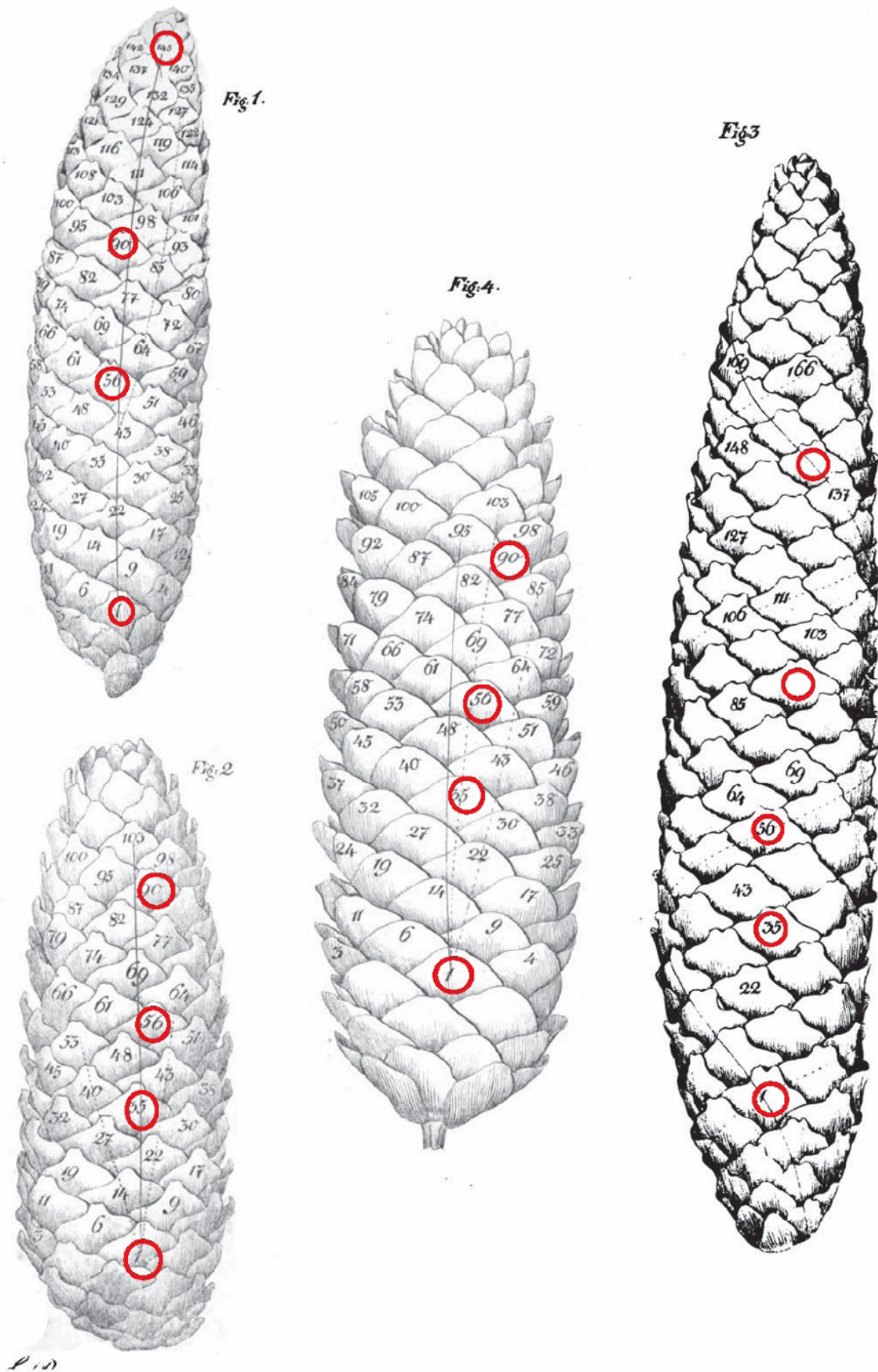


Fig. 8 Seed cones of *Picea abies*. (Left top) 8/21 rising to 13/34, (left bottom) 13/34, (center) 18/47, and (right) 21/55, according to Braun [36] (not copyrighted). The drawing at the center is a rare pattern that Braun found in more than a thousand cones. This pattern is almost the same as but slightly different from the normal patterns (8/21, 13/34, 21/55). To make it clear, scales differing by Fibonacci numbers are marked with circles by the author. The exceptional pattern (18/47) is overlooked if the pattern is classified with contact parastichy numbers. All patterns in this figure belong to the normal system 5:8.

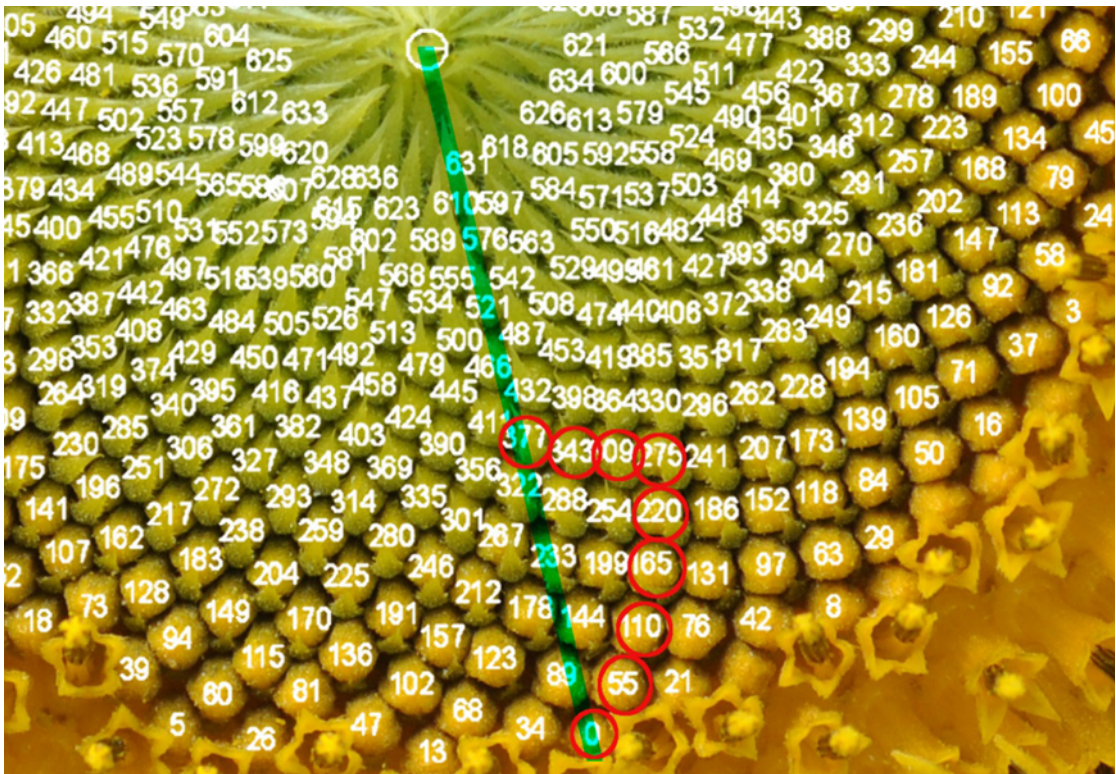


Fig. 9 *Helianthus annuus*, adapted from [37,67] (CC BY-SA 3.0). A path of circles (red) represents a graphical representation of $55 \times 5 + 34 \times 3 = 377$. Note that 233, 377, and 610 are Fibonacci numbers. Is it fortuitous that the end point 377 sits on the radial line through the initial point 0 (green)?

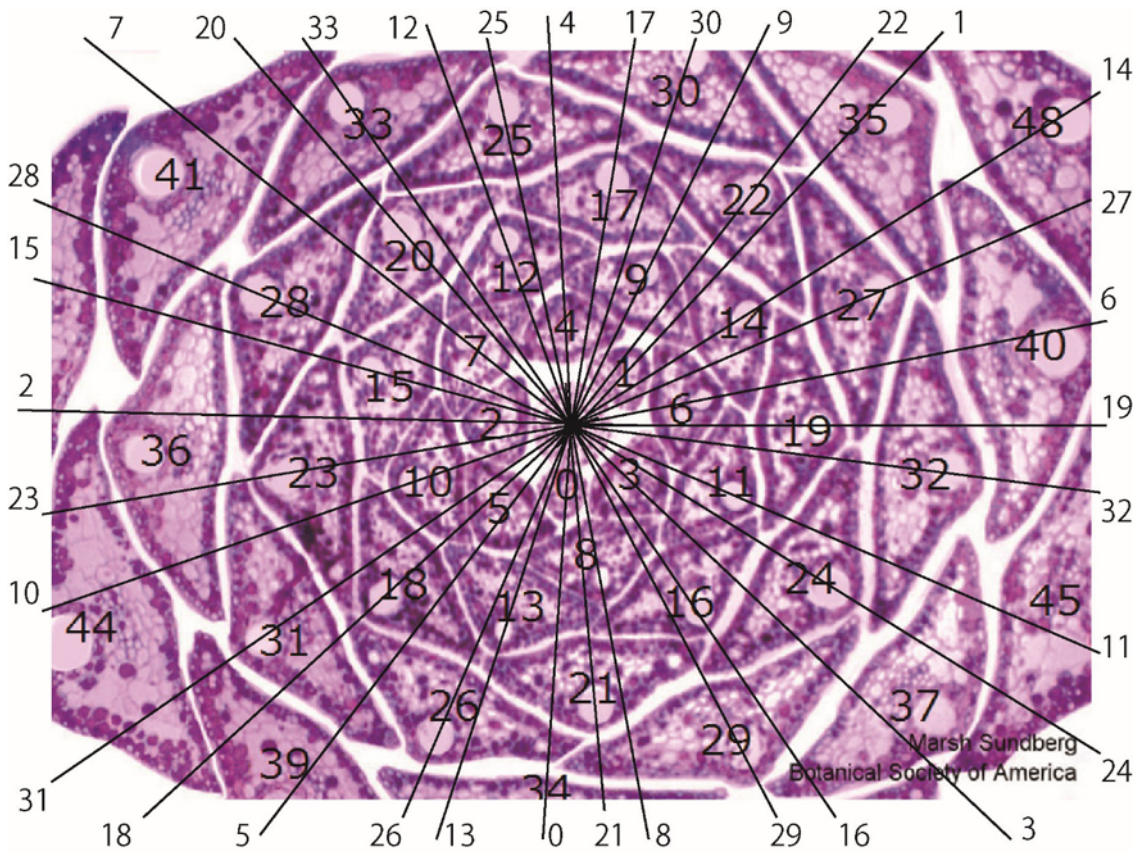


Fig. 10 *Sequoia sempervirens*, adapted from Marsh Sundberg [68] (CC BY-NC-SA 3.0). As indicated by radial lines, Leaf 0 arises in a direction between 13 and 21 (and even between 34 and 21) even though the latter are not in direct contact with 0. How do they know their correct position?

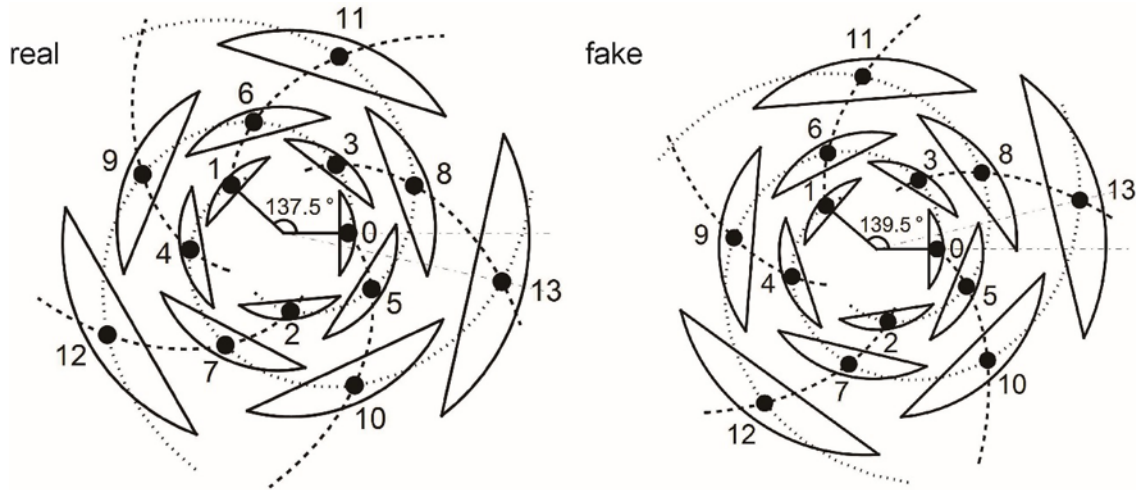


Fig. 11 Real and fake patterns to illustrate a subtle difference in divergence angle. Note the difference in position of 13. In the real pattern (137.5°), Leaf 0 occurs not only between 5 and 8 but between 8 and 13.

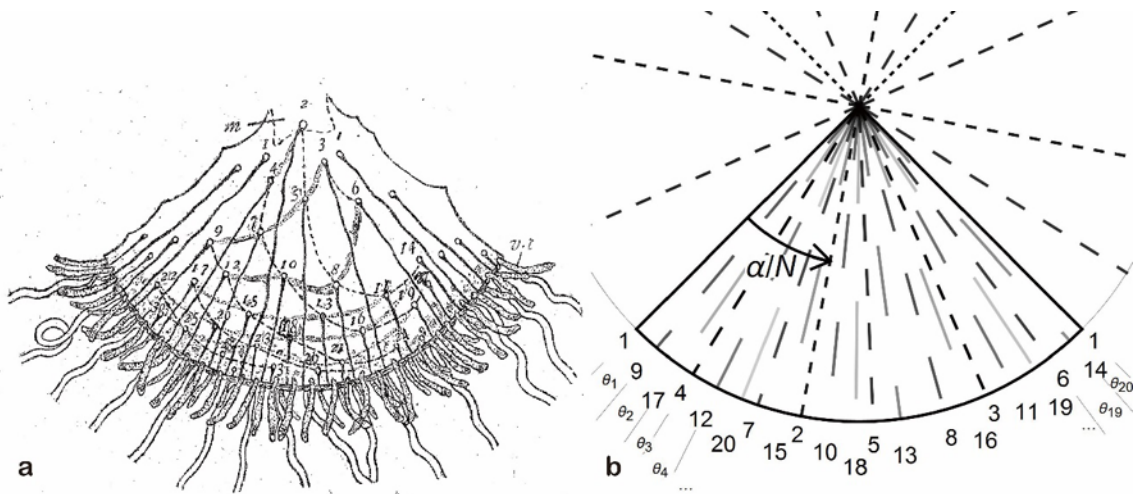


Fig. 12 Tentacles of jellyfish are arranged in accordance with the rule of spiral phyllotaxis. **a** Arrangement of ex-umbrella tentacles in a quadrant of a tetramerous ($N = 4$) specimen of *Olindias formosus*. Reproduced from Komai and Yamazi [38] (not copyrighted). **b** The theoretical arrangement in which consecutive organs are placed at constant intervals of $\alpha/N = (137.5^\circ \pm 1^\circ)/4$ conforms to the observed order, i.e., 1, 14, 6, 19, 11, 3, 16, 8, 21, 13, 5, 18, 10, 2, 15, 7, 20, 12, 4, 17, 9, 22, 1 [39], exactly the same order as shown in the circumference of Fig. 10.

corollary is that past papers must be critically revisited if they are ignorant of the prior German studies.

In 1948, Richards criticized the lack of understanding of phyllotaxis in English-speaking countries [50]. Considering his ironic tone, mathematical competence, and generally poor communication during this period, it is more probable that Richards was unaware of the advances made by Hirmer and others than that he did not give credit to them. Richards argues that divergence angles' close approach to 137.5° is apparently fortuitous [50: p. 225]. This view is apparently at variance with Hirmer's view. Decades later in 1974, Adler [15] cites Richards (1948) to resuscitate the old idea of Schwendener [51], according to which phyllotaxis is the necessary result of contact pressure of neighboring organs (Fig. 13). In 1951, Richards criticized Plantefol [52] by emphasizing the simple fact of the constancy of divergence angle: "One of the striking facts of phyllotaxis is that in most spiral systems the mean divergence along the genetic spiral approximates closely to the Fibonacci angle" [p. 513] and "the divergence proper along the genetic spiral remains substantially unchanged" [p. 514] (see also [p. 560] on "the apparently extraordinary exactness"). However, it appears not that he changed his view on how the constant angle is brought about [p. 519]. In any case, the fact remains that Richards did not refer to the German studies [53–55].

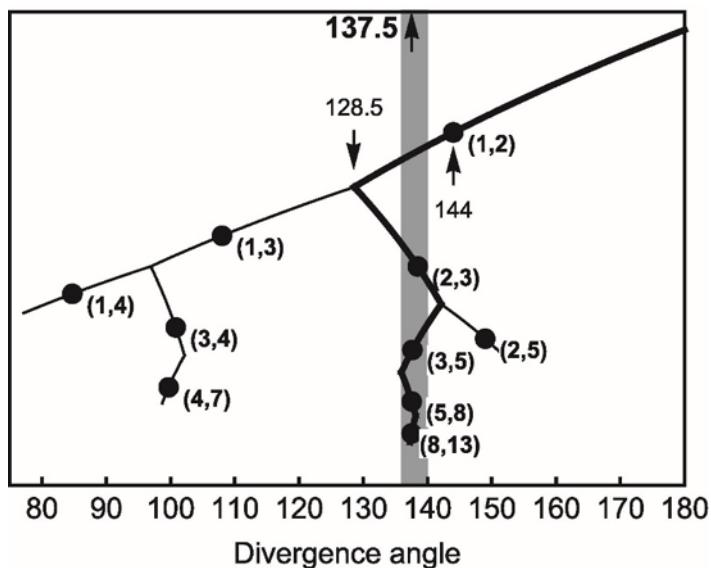


Fig. 13 A theoretical diagram for the range of divergence angles allowed for a given pair of contact parastichies (in parentheses) [1,51]. A dot indicates the predicted value of divergence angle when contact parastichies cross orthogonally. According to this model, the divergence angle of a (1,2) system may take any value between 128.5° (down arrow) and 180°, whereas it is given by 144° (up arrow) in the orthogonal (1,2) system. In striking contrast to the theoretical expectation, a shaded area indicates an observed range after Fig. 5 [30]. The discrepancy between theory and observation is remarked by van Iterson in 1907 [1: p. 247–252], by Snow in 1955 [12], and by Jean in 1986 [16].

In the first paper of a series of experimental studies, in 1932, Mary and Robert Snow make reference to Hirmer (1922) in a negative manner [56]. However, since then, two decades have passed before R. Snow appreciates the significance of Hirmer (1931) [6] and Fujita (1939) [30]. In fact, this review article in 1955 is concluded by remarking that accurate constancy of the 137.5° angle is the unsolved problem of phyllotaxis, on which a speculation is made about the biological advantage of this angle [12]. In 1962, this problem is recognized as a chief difficulty of their space-filling interpretation [13]. This paper informs us that at least some years ago Richards noticed a related difficulty. The regular arrangement in a space-filling model is unrealistically fragile, so that the theory needs to be supplemented with a regulation mechanism. In this paper [13], the Snows proposed that the exact regulation of the 137.5° arrangement is accounted for by means of consistent change in extension of leaf bases. Unfortunately, the Snows' late studies have not been referenced while their early studies are often cited as the founders of space-filling theory. Decades later, Jean has remarked the discrepancy between Fujita's results and Adler's model independently of the Snows (Fig. 5 and Fig. 13) [5,16].

The discussion in this section is not to discredit the past theories. It is intended to bring to light the prior studies ignored. Progress in phyllotaxis research has not followed a straight course. Consequently, it should be kept in mind that it is not unlikely for a new theory to contradict ignored observations.

Consequently, it should be kept in mind that it is not unlikely for a new theory to contradict ignored observations.

Evolutionary explanation

The uniqueness, persistent accuracy, and universality of the constant divergence angle are explained based on the evolutionary hypothesis that the apical divergence angle is a heritable trait adjusted by natural selection. Then the puzzle is that the survival value of 137.5° is not at all obvious. Indeed, the above observations imply that it does not exist in a particular pattern at a particular moment. The author argues that the special utility of 137.5° manifests itself only if phyllotaxis changes during an individual's life are considered. Fig. 14 illustrates a synthetic view of phyllotaxis. As leaf primordia develop, the spiral arrangement at the shoot apex changes over to a vertical arrangement of Schimper and Braun. Most commonly, the 137.5° arrangement changes over to 2/5, 3/8, or 5/13 on an elongated shoot. Imagine, hypothetically, what shoot patterns would occur if the initial angle were different from 137.5°. This problem is answered purely theoretically based on mathematical considerations. The unique significance of the 137.5° angle manifests itself by arranging the resulting sequence of fractions in a table format (Fig. 15) [57]. The 137.5° arrangement is the optimal initial arrangement with which to prepare for the subsequent phyllotaxis changes to occur on an elongating shoot. In fact, the 137.5° angle minimizes the effect of phyllotaxis changes during the individual's life (Fig. 16) [58]. Spiral arrangement of plant leaves and jellyfish tentacles provides us with an unusual example of convergent evolution, for the same arrangement is most likely to be reached independently of the taxonomy and physiology [39,58]. The angle 137.5° is best adapted to changing conditions. It is the best compromise, or the golden mean, if it is not the best choice in a particular condition.

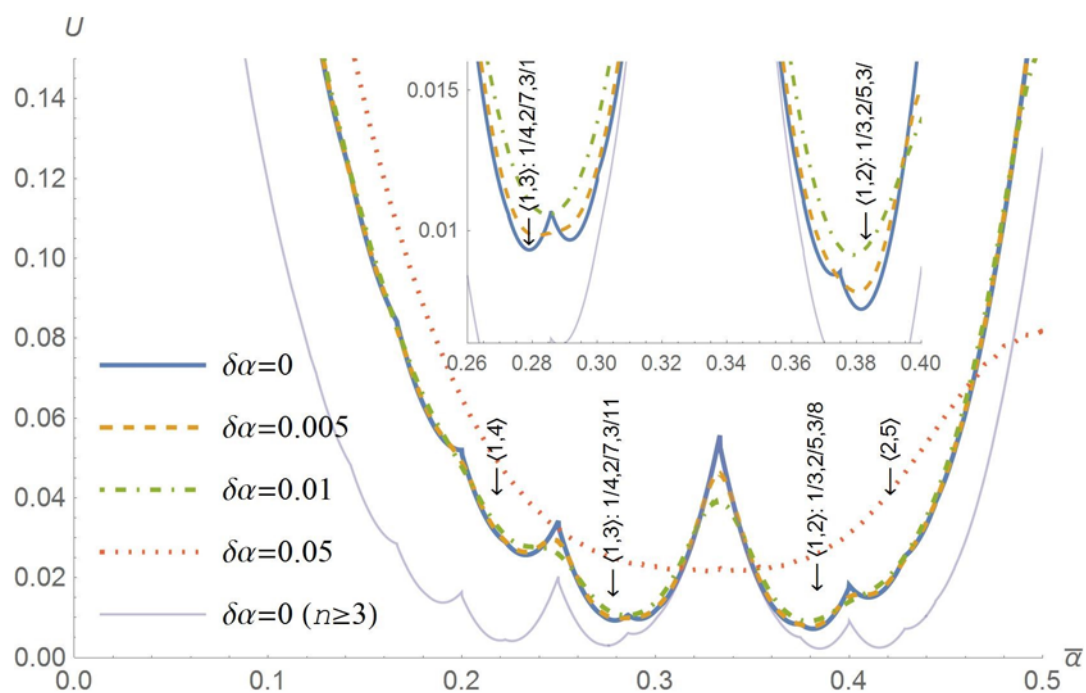


Fig. 16 The golden angle 137.5° minimizes the total cost of phyllotaxis change (CC BY 4.0) [58]. Change in shoot phyllotaxis causes a twist of the stem. The cost is plotted against the mean divergence $\bar{\alpha}$ for four values of the standard deviation $\delta\alpha = 0, 0.005$ (1.8°), 0.01 (3.6°), and 0.05 (18°). The inset shows the absolute minimum at $\bar{\alpha} = 0.382$ (137.5°) and the second minimum at 0.276 (99.5°).

Closing remarks

In the classical work *On growth and form*, d'Arcy Thompson wrote to the effect that Sachs regarded the whole doctrine of phyllotaxis as mere playing with mathematical ideas [59]. According to Richards, "Sachs himself, however, made no constructive contribution to the theory of phyllotaxis" [50]. On behalf of Sachs, it should be pointed out that he challenged the idealism of his time. As facts of observation, he accepted the common occurrence of shoot phyllotaxis of $1/3, 2/5, 3/8, 5/13$ as well as occasional transitions among them [60: p. 499]. In the same period as the empirical rules of shoot phyllotaxis were discovered, Louis and Auguste Bravais had insight into the presence of the universal constant 137.5° behind this phenomenon, where inference was made based on indirect observations backed up with their mathematical skills [24]. In effect, their analysis in 1830s is the first modern theory in phyllotaxis. The concept of the ideal angles must seem too idealistic to accept even today. With the advantage of hindsight, however, Sachs was wrong in criticizing the Bravais brothers that they assume the original divergence of 137.5° "which stands in irrational relation to the circumference of the stem, and from it all other divergences should be derivable; and this ultimately degenerates into mere playing with figures which in this form afford no deeper insight into the causes of the relations of position. As regards serviceableness in the methodic description of plants the theory of the brothers Bravais is much inferior to that of Schimper." [61: p. 169f]. In fact, the Bravais and Schimper are compatible as they observed different aspects of the same phenomenon. In contrast to Schimper and Braun, the Bravais as well as Hirmer judiciously refrained from arguing that much about the mechanism of phyllotaxis [6,24]. It is ironic that the mainstream botanists in the 19th century dismissed the Bravais based on speculation [61,62], whereas Hirmer and others acknowledged their pioneering insight based on direct observations.

The problem of phyllotaxis appears readily understandable without background knowledge. As a matter of fact, it is not as simple as it appears at a first glance. The number-related puzzles of spiral phyllotaxis come down to the problem of fine-tuning

or regulation. On a shoot apex of independent groups of plants, divergence angles between incipient leaves are actively regulated at a constant value close to 137.5° . I emphasized even more intriguing observation of its apparently unnecessary accuracy. The most fundamental question is whether or not evolution by natural selection is indispensable for understanding this mathematical regularity.

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