

Note on Phyllotaxis.

BY

ARTHUR H. CHURCH, M.A., D.Sc.,

Lecturer in Natural Science, Jesus College, Oxford.

—♦—
With two Figures in the Text.
—♦—

WRITERS on Phyllotaxis are generally agreed in accepting the series of formulae known as the Schimper-Braun series of divergences, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, &c., as fundamental expressions of the primary phenomena of the arrangement of lateral members. This series of fractional expressions, which involves the utilization of the Fibonacci ratio series 2, 3, 5, 8, 13, &c., has thus proved for over sixty years the ground-work of all theories of phyllotaxis, and is usually described in the early pages of textbooks. Taking the ' $\frac{2}{5}$ ' as a type of these values, this expression implies that in placing five members on a spiral which makes two complete revolutions of an axis, the sixth member is mathematically superposed to the first, and that successive members differ by a divergence-angle of 144° . So simple are these relations and so thoroughly well known that it is not necessary to dwell further on the vast superstructure of morphological theory which has been built up on this foundation. However, as a matter of fact, taking the $\frac{2}{5}$ divergence again as an example, it is beyond doubt that observation of the actual plant shows that these relations do not strictly hold, and various theories

[*Annals of Botany*, Vol. XV. No. LIX. September, 1901.]

have at different times been proposed to show why this should be so; these again agree in taking the fractional expressions as representative of some mathematical law, all deviations from which must be due to the action of secondary forces, real or hypothetical. Such speculations include the original prosynthesis theory of Schimper and Braun, various torsion and displacement theories, culminating in the contact-pressure theory of Schwendener. These various views have been recently critically examined by Winkler (Pringsh. Jahrb., 1901, Heft I).

Since the general plan of these investigations consists, however, in superimposing some new hypothesis on the original conception of Schimper and Braun, a strict analysis of the subject demands a preliminary investigation of the views of Schimper and Braun and the scientific evidence underlying these fractional expressions, which become translated into accurate divergence-angles of degrees, minutes, and seconds. So long have these numbers been accepted that it appears somewhat gratuitous to point out that these generalizations rest on no scientific basis whatever, and that what passed for evidence in 1830 does not necessarily hold at the present day. Thus Schimper and Braun elaborated these expressions of divergence on the plan of the original $\frac{2}{5}$ or *quincuncial* system proposed by Bonnet in 1754. The starting-point in dealing with phyllotaxis is therefore the elucidation of the exact point of view of Bonnet, which has determined the path along which all subsequent investigation has proceeded. Now Bonnet, who had the assistance of the mathematician Calandrini, studied adult axes only, and devised, as an expression of the facts observed on *elongated* leafy shoots, a helix winding round a cylinder and spacing out at equal angles five members in two complete revolutions, the sixth member falling on the same vertical line as the first; a simple mathematical conception was thus utilized to express the observed phenomena. The fact which Bonnet thoroughly understood, that on a plant-shoot the sixth leaf did *not* fall exactly over the first, but that the series formed by every fifth leaf itself wound along a spiral

path, was explained by an assumption which has exerted a powerful influence on subsequent speculations, that the plant in fact purposely destroyed the postulated mathematical construction, in order that the assimilating members might be given free transpiration-space without any overlapping. Generally speaking, but little real advance has been made in the investigation of the primary causes of phyllotaxis beyond these original views of Bonnet published nearly 150 years ago. It will be noticed that the fractional expressions of Schimper and Braun repeat the hypothesis of Bonnet in a more elaborated form; the Fibonacci series of ratios is introduced in full, but these are so associated as to still imply helices wound on cylindrical axes. However, as pointed out by the brothers Bravais, axes are commonly conical, dome-shaped, or even nearly plane, and on such surfaces the helices would be carried up as spirals of equal screw-thread, and thus become curves which in the last plane case are spirals of Archimedes. That is to say, by expressing the helix-construction in the form of a floral-diagram, the position of leaves being marked on concentric circles whose radii are in arithmetical progression, the genetic spiral becomes a spiral of Archimedes, and the *orthostichies* are true radii vectores of the system. Such a geometrical construction is implied in the Schimper-Braun terminology which postulates the existence of orthostichies as straight lines. At the same time, by drawing curves through the same points in different sequence, other spirals appear in the construction, and these, distinguished as *parastichies*, are similarly by construction spirals of Archimedes.

Such geometrical plans are given in textbooks, and are used for instilling a primary conception of the arrangement of lateral members; the fact that they do not always agree with actual observations is glossed over by the assumption of secondary disturbing agencies, as for example *torsion*.

On examination, these fundamental expressions are seen to be based on:—

1. The assumption of a special divergence-angle.

K k

2. The existence of accurate *orthostichies*: these latter following from the construction as being radii vectores of a spiral of Archimedes, the spiral again being derived from Bonnet's helix with parallel screw-thread.

Since helices and spirals of Archimedes are also commonly the result of torsion-action, the way becomes paved for the addition of theories of lateral displacement or torsion-effects, which are expected to produce secondary alterations in the original simple system of Schimper and Braun.

It becomes therefore necessary to test the basis of these generalizations, and to examine the possibility of checking by direct observation either the divergence-angle or the *orthostichies* themselves; and finally to compare the plane constructions by spirals of Archimedes and see how far these really do interpret the appearances seen in a transverse section of the developing system in the plant.

Such investigation shows that the hypotheses have no true basis, while the construction by spirals of Archimedes is a conspicuous failure. Thus, the divergence-angle is hopelessly beyond the error of actual observation on the plant, since the points from which the angles have to be taken must be judged by the eye; when, therefore, the divergence-angles are expected to be true to a matter of minutes and seconds in fairly high divergences, this becomes a matter of impossibility; and the Bravais showed in 1835 that it was in fact impossible to *disprove* the standpoint that there was only one angular divergence in such cases of normal Fibonacci phyllotaxis, namely Schimper's 'Ideal Angle' of $137^{\circ}, 30', 27''\cdot936$. Similarly, it is equally impossible to judge straight lines by the eye alone, and the existence of *orthostichies* in spiral phyllotaxis as mathematically straight lines thus becomes as hypothetical as the Schimper-Braun divergence-angles. In neither of the two methods used for the practical determination of phyllotaxis-constants is there then any possibility of accurate mathematical demonstration. Although the tabulation of appearances as judged by the eye may be taken as an approximately accurate version of the real

phenomena, it is clearly impossible to found any modern scientific generalizations on angles which cannot be measured, and lines which cannot be proved to be straight: it thus follows that all speculations based on the assumption of the Schimper-Braun series must rest on a purely hypothetical foundation which may at any time be overturned. Such expressions, as Sachs constantly pointed out, attempt to imitate the phenomena observed without giving any reason for such geometrical construction.

Again, taking the mathematical interpretation of the Schimper-Braun system, that the genetic spiral and the parastichies are represented by spirals of Archimedes, while the orthostichies are radii vectores, a simple geometrical construction in terms of these spirals should bring out either the truth or error of this hypothetical relationship of the lateral members.

Thus, from the equation to the Archimedean spiral ($r = a\theta$), it is easy to construct a pair of spirals whose variable a shall have the ratio of the parastichies observed on any given specimen. Take for example the $\frac{8}{13}$ system, the primary contact parastichies of which are 8 and 13; Fig. 2 shows such a system geometrically planned for a left-hand genetic spiral: the members along the twenty-one orthostichy lines differ by twenty-one, and fall on the mathematically straight radii vectores of the system. The intersections of these parastichy spirals mark the *points* at which the lateral members are inserted, and the views of Schimper and Braun included only the consideration of such points. It is clear, however, that if the spaces between the spiral planes are regarded as containing the members pressed into close lateral contact, as seen in the transverse section of a foliage bud, the appearance of the progressive dorsiventrality of such lateral members is very fairly *imitated*. The construction, in fact, becomes more and more like the appearances seen in the plant as the periphery of the system is reached, but the central part which includes the actual seat of development is very inadequately represented: thus, the areas become so relatively elongated in the

radial direction as they approach the centre that they cannot possibly represent any formation of primordia at the stem-apex, on which such members are well known to arise as fairly isodiametric protuberances. At the same time, it will be noticed that the Archimedean spirals by construction all fall into the centre and stop there, so that no room is left in the

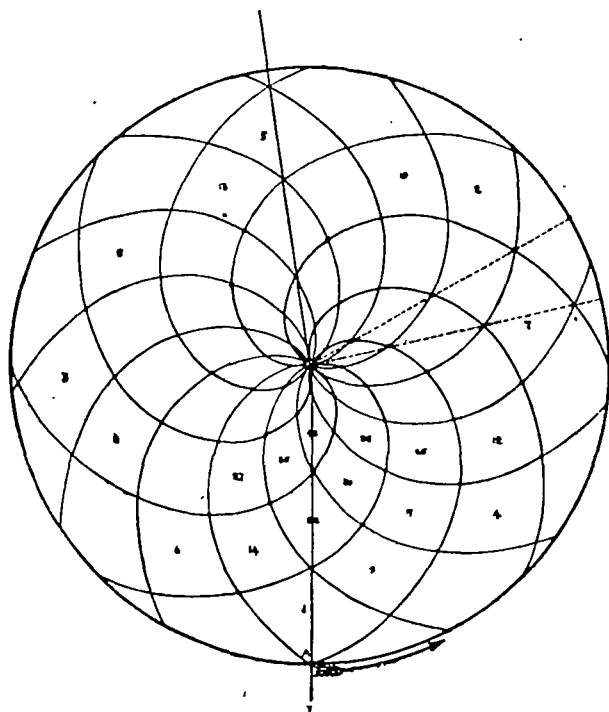


Fig. 2. Theory of Schimper and Braun. Construction for Phyllotaxis ϕ_T . OA . = Orthostichy line = radius vector passing through 1, 22, 43, &c. Members along the contact parastichies differ by 8 and 13 respectively. Genetic spiral winds left. Divergence-angle = ϕ_T of $360^\circ = 137^\circ 8' 34''$.

system for any subsequent growth and the addition of new members which naturally obtains in the plant.

Again, further consideration shows that all spirals, whatever their primary nature may have been, must necessarily pass

into Archimedean spirals, which differ by a constant along each radius vector, if they represent the limiting planes of members which grow to a constant bulk and then remain stationary, in the manner that lateral members do on the plant. The appearance of Archimedean spirals on adult shoots is thus secondary, and is merely the expression of the attainment of uniform volume by members in spiral series; it has nothing to do with the facts of actual development, during which lateral members arise as *similar protuberances*, which may be indefinitely produced without the possibility of the system being closed by a terminal member.

In other words, the genetic spiral must be regarded mathematically as *winding to infinity*, and being engaged in the production of *similar members*. That is to say, the possibility is at once suggested that the genetic spiral can only be represented by a *logarithmic* or equiangular spiral which makes equal angles with all radii vectores.

Not only is this a mathematical fact there is no gainsaying, but the introduction of log. spirals into the subject of Phyllotaxis at once opens up wide fields for speculation, in that these spirals are thoroughly familiar to the mathematician and physicist; representing the laws of mathematical asymmetrical growth around a point, they constitute in Hydrodynamics the curves of spiral-vortex movement, while their application to Magnetism was fully investigated by Clerk Maxwell. The possibility that the contact parastichies may be also not only log. spirals but log. spirals which intersect orthogonally, and thus plot out a field of distribution of energy along orthogonally intersecting paths of equal action, is so clearly suggested that it may at once be taken as the groundwork of a theory of phyllotaxis more in accordance with modern lines of thought (cf. Tait, 'Least and Varying Action,' article *Mechanics*, Enc. Brit., vol. 15, p. 723).

A geometrical construction in terms of such spirals in the ratio (8 : 13) (Fig. 3) may be taken as a representative system corresponding to the preceding phyllotaxis-plan of Fig. 2.

It is difficult to avoid the conclusion that the log. spiral

construction gives the true key to the problem, and that the whole subject thus becomes a question of the mechanical distribution of energy within the substance of the protoplasmic mass of the plant-apex: that phyllotaxis phenomena are the result of inherent properties of protoplasm, the energy of life being in fact distributed according to the laws which govern

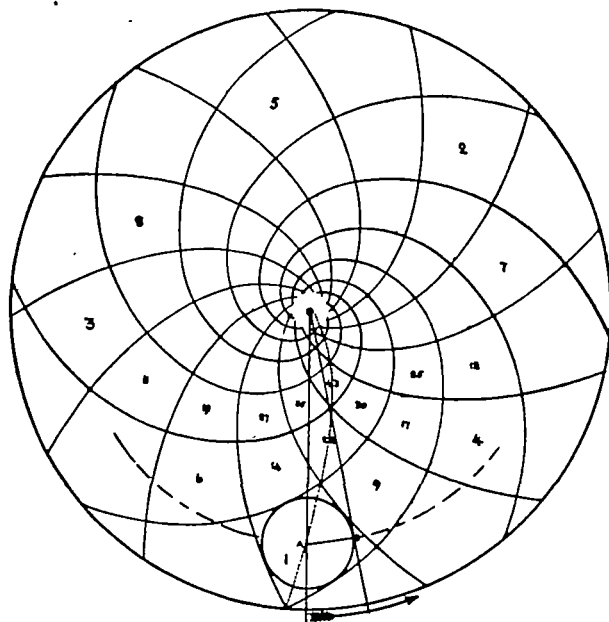


Fig. 3. Log. spiral theory: Construction for Phyllotaxis system (8+13) in terms of distribution of energy. Contact Parastichies = orthogonally intersecting log. spirals in ratio (8 : 13). The curve through 1, 22, 43, &c., is also a log. spiral. Genetic spiral winds left. Divergence-angle = $137^{\circ} 30' 38''$. Bulk-ratio of axis to primordium = $OA, AB. = 1 : 5$ within a small error, or $= \sin AOB = .204$ for the true curve.

the distribution of energy in any other form: and that the original orthogonal planes, the relics of which survive in the contact parastichies of the system, represent the natural consequence of a mechanical system of energy-distribution directly comparable with that which produces the orthogonal intersection of cell-walls at the moment of their first formation,

which was deduced by Sachs from the analogy of the orthogonally intersecting planes of thickening observed in cell-walls and starch-grains.

The readiness with which the several problems of phyllotaxis may be solved from this standpoint, when once the key to the whole subject is grasped, is very remarkable, and these views have been elaborated to considerable length in a paper which awaits publication. The results are so varied and striking that it is difficult to give any summary of them in a small space: based as they are on the relative value of the spirals of Archimedes and logarithmic spirals as interpreting the true developmental spiral of the plant-apex, it is evident that the discussion of such curves is beyond the province of the non-mathematical botanist. The object of the present note is therefore merely to point out that the subject of phyllotaxis thus enters entirely new ground which promises results more fundamental than any yet obtained in the domain of plant morphology: for example, it follows in such constructions that an equation may be given for the plane section of a lateral primordium which will serve as a true mathematical definition of a leaf, differentiating it from a stem: the true divergence-angles may be calculated, and a definite numerical value can be given to the ratio $\frac{\text{axis}}{\text{primordium}}$ which determines any given system; while the geometrical constructions, on the plan of Fig. 3, have the advantage that they do agree with the appearances observed in the plant; they obey and amplify Hofmeister's law, and from the standpoint of energy-distribution afford the clue to the subsequent building up of the elaborate 'expansion-systems' of which the capitulum of *Helianthus* may be taken as a type.

It is not proposed at present to go into further detail as to these questions which are very fully discussed in the paper already prepared for publication; until logarithmic spirals are more familiar to the botanist it will be sufficient to point out that the true key to phyllotaxis is undoubtedly to be found in the solution of the problems of symmetrical or asymmetrical

distribution of energy in orthogonally intersecting planes around an initial 'growth-centre'; in the latter case the whole of the spiral paths are log. spirals. The perfection of such a construction involves uniform growth in the system; and owing to the obvious impairment of this uniform rate of growth behind the plane portion of the apex, the true log-spirals are possibly never to be observed on the plant, although the approximation has been found in certain cases to be extremely close. Ultimately all these curves pass into spirals of Archimedes as the members cease growth on the attainment of constant volume, and these latter curves therefore occur on adult axes and appeal to the eye in the macroscopic view of the entire shoot. They were thus correctly isolated by Bonnet, to whom the detailed construction of the growing point was naturally unknown in 1754. The curves seen in transverse section of an apical system of developing members are thus probably curves transitional between log. spirals and spirals of Archimedes.

On the other hand it will be noted that the new constructions are equally incapable of absolute verification by any angular measurements on the plant; Schimper's orthostichies have vanished, as pointed out by the Bravais, for the more general examples of phyllotaxis, and the difference between the two spiral systems is very slight to the eye: but, while the Schimper-Braun School only sought to imitate the appearances seen on the plant, the log. spiral theory gives at least an equally correct summary of the facts observed, and is in addition founded on definite mechanical laws of construction by orthogonal trajectories which have already been accepted for plant anatomy; it is so far then the logical outcome of Sachs' theory of the orthogonal intersection of cell-walls, and represents therefore another special case of the distribution of energy along planes of equal action¹.

BOTANIC GARDENS, OXFORD.

May, 1901.

¹ Cf. Church, On the Relation of Phyllotaxis to Mechanical Laws. Part I, Construction by Orthogonal Trajectories. 1901.