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ON THE INTERPRETATION OF PHENOMENA
OF PHYLOTAXIS

By

A. H. CHURCH, M.A.

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ON THE INTERPRETATION OF PHYLLO- TAXIS-PHENOMENA

I

INTRODUCTORY

IT is now some time since a hypothesis was put forward¹ which apparently suggested reasonable probability for regarding the general phenomena of rhythmic patterns presented by phyllotaxis-constructions in the great majority of higher plants as referable to propositions involving equal distribution of energy in the growing plant-apex, with the result that the contact-parastichies which map the scheme are to be regarded as affording a clue to an orthogonal system of certain segmentation-paths in the living substance of the growing-point, taken as a whole, without any regard to its secondary subdivision into component cells. The view is at first sight so simple, and commends itself so readily to any one conversant with the general appearance of a transverse section taken through a system of growing leaf-members at a stem-apex, more especially in cases in which there is little disturbance of the primary construction, that it might be thought that it would have directly appealed to any botanical observer, from the standpoint of the analogy of centric geometrical constructions for distribution of lines of equipotential. But it is at once obvious that no amount of general resemblance can add anything to the value of the hypothesis as a scientific theory unless some proof can be afforded, or suggested, as implying a reasonable basis for further progress in the subject. The work in question² was not published until such a suggestion of probability was forthcoming; and the initial difficulty of the problem, in fact, consists in determining to what extent any true proof may be possible; since angular measurements on actual plant-specimens, or on careful camera-lucida drawings of sections, can never hope to come within a range of accuracy admitting of an error of less than half a degree, while precise mathematical theory soon begins to tabulate minutes and seconds. However, taking the mathematical deduction of the theory as involving a divergence-angle of approximately $137\frac{1}{2}^{\circ}$ for all Fibonacci ratios of (2 : 3) and over, it is remarkable how nearly this angle is approximated in actual measurements of sectional drawings taken from apices presenting such phyllotaxis-formations.

The method of proof, admitted as the only one possible under the circumstances, consisted in assuming the fact of orthogonal construction as presented in systems involving a simple condition of uniform growth, and passed on to the deduction of equations for the sectional outline of theoretical primordia involved in such plant-constructions, and the examination of their geometrical properties. To these curves the name '*quasi-circle*' was given,³ and the form of several of these curves (including those specially interesting as differing to the eye from the shape of a true circle)

¹ Church (1901), Ann. Bot. xv, p. 481, 'Note on Phyllotaxis'; (1904), 'On the Relation of Phyllotaxis to Mechanical Laws'; (1904), Ann. Bot. xviii, p. 227, 'Principles of Phyllotaxis'; Cook, (1914) 'The Curves of Life', p. 81.

² Rel. Ph. Mech. Laws, loc. cit., p. 350.

³ loc. cit., p. 329. Fig. IX.

was plotted and figured for reference.¹ The remarkable fact was obtained from the mathematical review of the problem, that *all such curves are necessarily symmetrical with regard to a radius of the system, whether the construction-lines are spiral or circular.*² From this fact the conclusion was drawn that, since these remarkable properties were common to the quasi-circle figures of the uniform growth construction, and also to the typical leaf-forms of plant-life—in that the quasi-circle possesses the ‘dorsi-ventrality’ as well as the ‘isophylly’ of a foliage-leaf under all circumstances of normal centric distribution³—one is legitimately entitled to assume that the mathematical facts afford so strong an inherent probability of actual agreement, that the hypothesis is well-supported, and is entitled to further extension along similar lines. So far, then, it would appear that the *general proposition of uniform growth*, involving primordia of the type of the quasi-circle, affords a firm foundation for obtaining the first fundamental views of the mode of approaching the subject of the mechanism of leaf-form in the plant-kingdom; and this should be capable of transference to the theory of the construction of all lateral growths included in living organisms under the term ‘appendages’.

Since problems of phyllotaxis attract little attention at the present time, when there is so much to assimilate in other branches of the science, and the introduction of an excessive amount of mathematical calculations renders the subject distasteful to the general botanist, who possesses a healthy scepticism as to the capacity of plant-life for restricted mathematical presentation; and while the subject of formal morphology still remains obscured under such infinite complications of biological specialization, that many have lost hope of any scientific presentation of the fundamental factors of plant-form as may have been outlined by the older writers on morphology; and we, so to speak, no longer see the wood for the trees; it may be well at the present stage to summarize the points in favour of the present theory, and to state concisely the difficulties of the subject as well as its advantages and suggestions. As the mere mention of Tangential, Equiangular, or Logarithmic Spirals, the curves utilized in these preliminary constructions, suffices to throw the non-mathematical botanist off the subject, the idea may be conveniently summed up as the *Equipotential Theory of Phyllotaxis*; thus indicating in one word the necessary essential geometry of the constructions, and the suggestion of the Physiological Mechanism of the production of the patterns; while it also covers the wider case in which the construction may be presented in terms of straight lines and circles (whorls), as well as the more complex and changing systems.⁴

The Equipotential Theory, if it then be so termed, in order to avoid any introduction of the word *spiral*, which has led to so many pitfalls and futile discussions, makes no new assumptions whatever, beyond features regarded as fundamental by the recognized leaders of the past. Thus principles of orthogonal construction were first demonstrated in the plant by Sachs, though not in this particular connexion; and the existence of orthogonal series of leaf-appendages was assumed, though not proved by Schwendener.⁵ Again, while the full interpretation of all space-form is necessarily based on the mathematics and geometry of three dimensions,

¹ R.P.M.L., p. 336.

² loc. cit., p. 332.

³ loc. cit., p. 332.

⁴ loc. cit., pp. 111, 174.

⁵ Sachs (1887), ‘Physiology of Plants’, Eng. Trans., p. 497; Schwendener (1878), ‘Mechanische Theorie der Blattstellungen’: Weisse, in Goebel’s ‘Organography’ (1900, Eng. Trans.), p. 74.

and the elaboration of a plant or animal growth-form in the case of higher organisms is still, from our elementary standpoints, an infinitely complex phenomenon, there is no reason why the first fundamental principles should not be firmly established; and in the application of the Equipotential Theory to plant-phyllotaxis we have at hand a remarkable series of special cases of centric space-distribution which may afford a clue to far wider problems. No apology need be offered for the introduction of a theory which is undoubtedly destined to have a brilliant future as one of the most fundamental features of biological science. Just as Plant Physiology may be defined as the study of the controlling effect of Plant-life on the laws of Physics and Chemistry, and modern physiologists are continually stating, often with wearisome iteration, the obvious truth, that every plant-mechanism consists of, and works in terms of, chemical 'molecules' beyond the range of vision;¹ so the study of Formal Morphology may be regarded as that of the similar directive effect of living matter following the laws of Geometry; the ultimate expression of which may again come under the head of molecular arrangements and groupings, with the laws which determine them. The possibility is not wholly eliminated that in dealing with physiological processes there may be other agencies beyond molecular organization, but at the present time it is difficult to get beyond the molecular outlook, and this remains the centre of attack. That is to say, when the relations of visible primordia and cell-units fail to give an adequate explanation of phenomena of form and structure, the next step will be the elucidation of the possible molecular organization of the protoplasm itself. This in turn may fail, in the examination of vital phenomena, and the solution of the problems be removed some stage further on. But at the present day we are still approaching molecular phenomena and have as yet no conception of their limit. It was from this standpoint that the equipotential theory was originally put forward. Once Phyllotaxis is removed beyond questions of mechanical contact-pressures of primordia and cell-segmentation, the question of more intimate physical factors becomes the next point of attack. There is no other choice.

Reference may be also made to other papers dealing with the primary problems of leaf-origin within more recent years; the most important being, perhaps, a volume by G. van Iterson, jun. (1907),² covering a wide range of abstruse mathematical speculation. The principles of the log spiral constructions are recognized as essential, from the standpoint that any centric distribution of 'similar figures' must be inevitably expressed in equiangular spirals; similarly, ratios of the contact-parastichies are adopted as the simplest method of describing the patterns. Apart from mathematical considerations, however, the most remarkable feature is the departure from the principles of orthogonal construction, previously postulated as alone likely to throw light on any essential mechanism of the process, and an attempt is made to combine the 'contact-pressure' theory of Schwendener with a corrected mathematics (*loc. cit.*, p. 291). A visible primordium is assumed, based on a wholly speculative 'folioid'-effect, as a curve supposed to imitate the general form of a leaf-section, without any very convincing reason being adduced as to why the projection of a horizontal circle on a cone-surface should do so (both circles and cones being wanting at a plant-apex). Log spiral systems of such similar folioids (p. 161) are put forward as suggestively approximating the appearance of bud-sections. The application of

¹ Czapek (1911), 'There is nothing to indicate that the phenomena of life are ruled by forces which are different from chemical and physical energies in inanimate nature'.

² Van Iterson (1907), Delft, 'Mathematische und mikroskopisch-anatomische Studien über Blattstellungen', pp. 1-331.

these views to Schwendenerian systems of contact-pressures and the origin of lateral buds affords no clearer presentation of the subject than was previously available; but it may be noted that a valuable contribution to botanical literature was afforded in the recognition for the first time in a botanical work of the systems of organization, closely comparable so far only as relating to geometrical spiral systems of similar figures, and similarly involving patterns with quite definite Fibonacci relations, which occur among holozoic Protista in the sea (as certain types of Foraminifera, loc. cit., p. 300).

For the continued support of contact-pressure theory, and complete misconception of what the Equipotential Theory is meant to do, cf. Weisse¹ (1903) *Prings. Jahrb.* xxxix, p. 416.

Schoute (1913)² adopts the notation of the $(m+n)$ type, but follows Iterson and the contact-pressure theory of Schwendener, in speculations which get further away from observation of the actual conditions at the plant-apex, with special reference to a type of curve termed a 'Pseudoconchoid'.

The great difficulty of phyllotaxis discussions appears to be to steer clear of mathematics and take facts as given by actual plant-forms; since facts of observation may be correct if the interpretation prove wrong. In looking over such schemes as those of Schoute (pp. 268, 270, 277), or Iterson (Taf. I, IV, V, VI, X, XII), one can only wonder what on earth these things have to do with plant-form, and the older criticism of Sachs as to 'playing with figures' acquires a new significance.

The essential theory behind Phyllotaxis deals with the causes of leaf-origin, the meaning of what is implied by a 'leaf'-extension of the plant-soma, its phylogeny and secondary adaptations; packing within a secondary bud-construction, secondary changes and irregularities in the scheme of arrangement, and the working out of complex leaf-form as the expression of phenomena of *retarded unilateral growth*, are very subsidiary to the main points at issue.

II

THE GENERAL PRINCIPLES OF PHYLLOTAXIS³

BEYOND the vague attraction of the presumed mystical and decorative properties of spirals which appealed to early human intelligences,⁴ in the absence of any knowledge as to the geometry of such constructions (beyond

¹ Weisse (1903), *Prings. Jahrb.*, p. 416.

² Schoute (1913), 'Über Pseudokonchoiden'. *Rec. de Trav. Néerland.* x, p. 153.

³ Church (1904), 'On the Relation of Phyllotaxis to Mechanical Laws', pp. 353, 112 figs.

The following short summary of a previous memoir, on the general nature of the growth-problems to be dealt with in the consideration of the shoot-systems of higher plants, may serve as a convenient introduction to a subject which is admittedly not only complex and involved, but has been made needlessly so by many more mathematical writers, and is still little known to botanists who have been largely content with the barest outline of the simpler and more superficial phenomena.

The examination of much of the detail is certainly tedious to many to whom a pseudo-mathematical presentation is often a deterrent, and inferences have been frequently drawn from gratuitously introduced and wholly empirical mathematical premises, which are little justified by the facts observed in plant-constructions. At the same time there can be no doubt that the subject, sufficiently interesting in itself to be a delight to the investigator of organic and inorganic space-form, has a greater value as the only available stepping-stone to a more comprehensive know-

Archimedes), culminating in such abstractions as the Spiral Theory of Goethe's Nature Philosophy,⁵ of which traces persist to modern times—the first step in the more distinctly botanical investigation of spiral growth-forms begins with Bonnet⁶ who first distinguished, though without any strictly geometrical presentation, the familiar *quincuncial system*, as the '½ spiral', in terms of a helix winding on a cylinder, which has done duty in elementary text-books to the present day, and has been commonly regarded as a sufficiently satisfactory statement of the facts of normal leaf-arrangement, so far as the non-mathematical student is concerned⁷; all further discussion involving fantasies, possibly pleasing to the mathematician, but remote from any practical application in physiological botany,⁸ and to be relegated to cranks of minor scientific importance.⁹ In the more obvious facts of observation on plant-constructions considerable progress was made in France by the brothers Bravais¹⁰; but the more modern statement of the problems followed the more popular presentation of the subject by Schimper¹¹ and Braun (1830-35) of the rising German school¹²; and it is with the introduction of German botanical books that general conceptions have been inherited by modern writers.¹³ It is interesting to note that Schimper and Braun really added little to the fundamental conception of Bonnet and Calandrini of some eighty years previously, but merely elaborated the same helical constructions, introducing

ledge of what has been included under the vague ideas of 'growth' and 'form' by morphologists.

Academic standpoints, whether in morphology, anatomy, or systematics, still play a considerable part in a science which should be a record of phyletic progression; and it is often only after wearisome wanderings through such labyrinths that one may find the clue to what really lies behind. A few illustrations expressing some of the more important features have been taken from the same work (Figs. I-XI).

⁴ T. A. Cook (1903), 'Spirals in Nature and Art'; (1914), 'The Curves of Life', p. 266.

⁵ Goethe (1831), 'Spiraltendenz der Vegetation', p. 194; Sachs (1890, Eng. Trans.), 'History of Botany', p. 159.

⁶ Bonnet (1754), 'Recherches sur l'usage des feuilles dans les plantes', pp. 164-188.

⁷ Prantl and Vines (1881), 'Text-book of Botany', p. 7; Vines (1895), 'Students' Text-book of Botany', p. 27; Strasburger (1912, Eng. Trans.), 'Text-book of Botany', p. 41; Bower (1919), 'The Living Plant' p. 171.

⁸ Sachs (1875, Eng. Trans.), 'Text-book of Botany', p. 174, footnote; (1887, Eng. Trans.), 'Physiology of Plants', p. 501.

⁹ From such purely academic and pseudo-philosophical lines of approach the subject had attained a bad name, even among botanists; and this was not improved in more recent times by the writings of Schwendener and his opponents. Much futile speculation even in modern papers, more especially in discussions of the relations of floral constructions, might have been avoided by a clearer recognition of the elementary laws of phyllotaxis-phenomena.

Cf. also Airy (1874), Proc. Roy. Soc. xxii, p. 297; Henslow (1875), Trans. Linn. Soc. ii, Vol. I, p. 37.

¹⁰ Bravais (1837), Ann. Sci. Nat. Bot., pp. 67-71; C. de Candolle (1865), 'Théorie de l'angle unique en Phyllotaxie', Archiv. des sci. phys. et math. xxii, p. 199.

¹¹ Schimper-Braun (1835), 'Flora', pp. 145, 737.

¹² Sachs, 'History of Botany', loc. cit., p. 162; a clear account of all older views is given by C. de Candolle (1881, Geneva), 'Considérations sur l'étude de la Phyllotaxie', Archiv. des sci. phys. et math. v, pp. 260, 358.

¹³ Sachs (1875, Eng. Trans.), 'Text-book of Botany', pp. 167-181; Schwendener (1878, Leipzig), 'Mechanische Theorie der Blattstellungen': (1898), Gesamte Bot. Mitt. i, p. 105.

the full series of the ratios of the Fibonacci series (or any other summation-series),¹ and expressing their 'fractional divergences', and mathematical schemes in a manner which has proved the joy of generations of elementary mathematicians, much as the Linnaean System of Classification satisfied generations of simple-minded systematists, and has contributed to the irritation of those looking for first causes in plant-morphology. Thus Sachs,² as the leading text-book authority of the middle nineteenth century, dismissed the subject as 'playing with figures', yet failed to see that though such properties of numbers do express some rhythmic law, it is the factor inducing such rhythm which is the more fundamental problem of physiology. The attitude of the general botanical public has been admirably stated by Harvey-Gibson³ (1919), as he recalls 'the miseries endured in endeavours to master what was regarded as one of the articles of a botanist's faith'.

Yet there can be no doubt that behind such facts there must be one of the most fundamental laws of living plasma,⁴ the correct appreciation of which may open up the way to a clearer comprehension of what is included under the expressions *growth* and *form*; since all growth and all form in living organism must have had some beginning, and plant shoot-systems do not come 'by Nature', ready-made.⁵

The observations of Bonnet and Bravais, Schimper and Braun, by the limitations of their age, were necessarily devoted entirely to the description of effects noted on *adult* plant-shoots—with no reference whatever to the causation which might have produced them. To our ideas, the subject,

¹ Van Tieghem (1891), 'Traité de Botanique', p. 55; Sachs (1875), Text-book, p. 181.

² Sachs (1887, Eng. Trans.), 'Physiology of Plants', pp. 497-499.

³ Harvey-Gibson (1919), 'Outlines of the History of Botany', p. 98.

⁴ Church (1919), 'The Building of an Autotrophic Flagellate', Bot. Mem. 1, p. 11, 'Polarity and Surface Tension'.

⁵ A recent authoritative, if non-botanical, pronouncement on the subject by D'Arcy Thompson ('Growth and Form', 1917, pp. 634-651), is also of special interest as setting up views derived from ancient literature for the sake of knocking them down again, rather than for any reference to work on plants themselves. A pseudo-mathematical disquisition by Tait (1872), which has nothing whatever to do with the way a plant is made, is utilized (p. 645) to explain the 'numerous coincidences' and 'mysterious appearances', until 'we come without more ado to the conclusion that the Fibonacci series and its supposed usefulness, and the hypothesis of its introduction in plant-structure through natural selection, are all matters which deserve no place in the plain study of botanical phenomena'.

After all, the ratios do occur, and must be 'useful' for something; the chances are that their 'curious mathematical properties' do afford a clue to their meaning; 'mutation and natural selection' cover the only means known to science of determining why one plant should show them and not another, as specific, generic, or even family 'constants'. It is also the privilege of the botanist to investigate anything he comes across in the plant whether plain or ornamental.

For example, it is difficult to explain to the non-botanist that Phyllotaxis does not consist solely in speculating on the appearance of Pine-cones or Sunflower capitula; the former are of interest only as a special case, visible to the naked eye, of the obscure constant (a Fibonacci ratio) controlling the growth and space-form of every leafy shoot of every Pine-tree; and the disk of the Sunflower similarly visualizes a mode of construction controlling the growth of the vegetative apex, and so far the morphological organization of the entire plant. Other trees and plants may show other constants equally established, and probably 'useful', dominating the vegetative space-form, as the decussate symmetrical system of the Ash, Sycamore, *Aesculus* and *Buxus*; though some of these (Sycamore, *Aesculus*) may present vestigia of Fibonacci ratios in their floral organization.

like many others, was thus approached from the wrong end; it was even established and expressed in literary form in complete ignorance of what the plant was really doing; so that not only does the entire superstructure rest on no adequate foundation, but its more essential problems become curiously obscured and muddled for any subsequent analysis.¹

Modern Botany has little to do with the effects which appeal to the eye on an adult plant-shoot. It seeks to determine how these phenomena originated—what is the mechanism of their production, what factors lie behind the mechanism, and how it was originally called into operation; that is to say, for what original function, or by what response to conditions of external environment. In dealing with such a subject in the most elementary manner, it is thus necessary to take an unbiased and wholly fresh start, and begin it again from a different point of view.

Leaf-arrangement is a function of the 'growing-point' of a 'stem'; phyllotaxis is the problem, not of the final appearance of the leaves on a shoot, but of the *origin* of such lateral appendages at the plant-apex—the discussion of the causes which lead to the inception of a primordium before it becomes visible as the slightest protuberance of the cell-tissue of an apex. The subsequent fate of the primordium, or its behaviour under contact-pressures, is a wholly irrelevant and secondary detail to be considered later. For example—the attainment of the adult condition in members which become equal in volume, or are equally spaced by secondary internodal extension, may lead to *helical* effects on the adult axes, which are wholly secondary. Similarly all interpretation of such effects in the transverse dimension, as plane figures, may be expressed in terms of *Spirals of Archimedes*, of equal and uniform screw-thread, which clearly have no reference whatever to the initial factors of a growing system of unequal units. That the whole geometrical and mathematical conception of phyllotaxis-relations should have been originally expressed in terms of Archimedean notation, was the necessary limitation of Calandrin, Bravais, Schimper and Braun, who knew no other mathematics of spiral constructions; and the subject once started on these lines followed on to modern times, without it occurring to anybody to point out such a fundamental error.²

Once it is understood that phyllotaxis involves phenomena of *growth* at a growing and expanding apex, it is necessary to introduce conceptions of mathematical growth, as studied, for example, in the growth of the electrical field, and see to what such generalizations may lead. The general mathematical proposition of a field of uniform growth about a point (centric), as represented by a circular meshwork of 'quasi-squares', is at once illuminative; since it not only gives certain effects of spatial distribution in terms of straight lines and circles, but it provides for the intelligible introduction of 'growing' logarithmic (or equiangular) spirals, in a system which is undergoing uniform expansion, and to which the phyllotaxis-phenomena of a growing apex must be obviously referable in the first instance, however much such a simple mathematical postulate may prove incapable of expressing all the facts of a living organism. Plant-form is not a simple subject, to be readily attacked by the expert mathematician; certain form-relations may appear at first sight simple, and have so appealed to many botanists since the time of Nehemiah Grew (1682)³; just as any child with a compass may draw a 'whorl of 6 leaves in a circle'; or even

¹ Schwendener (1878), 'Mechanische Theorie'; Weiss (1900) in Goebel's 'Organography', Eng. Trans., i, p. 75.

² Church (1901), Ann. Bot. xv, p. 481.

³ Grew (1682), 'The Anatomy of Planes', p. 152. 'So from the contemplation of Plants, men might first be invited to Mathematical Enquiries': Tab. 43-47.

further back, as in speculations by Kepler¹ on the occurrence of pentamerous symmetry in flowers, and observations on spirals by Leonardo da Vinci. In dealing with biological phenomena, the most elaborate human mathematics still fail hopelessly in touching such problems; yet the initial steps must be simple and readily followed; complexities come later, and require to be taken step by step as in the Newtonian laws of motion.

Comparison of such a scheme of uniform growth-expansion about a point (centric and two-dimensional), with consequent possibilities of orthogonal construction-lines, as expressing lines of equipotential (as in a static electrical field), or of lines of equal pressure and flow in circular or spiral vortices of fluid motion,² is also illuminating as expressing a convenient geometrical method of 'transformation'. Thus by using such a framework of 'squares' it is readily possible to transform any circular scheme into a spiral 'homologue', or *vice versa*; and again by added complexity to express the corresponding *eccentric* homologues of either centric or spiral systems.³ But such mere mechanism of transformation, though immediately interesting as exhibiting the true botanical relation, so long misunderstood, of the essential geometrical relation of spiral and whorled phyllotaxis, so widely distributed in the plant-kingdom, is but a small part of the range of the subject. The essential significance of the construction of such a field of growth, is that it is *growing*; i.e. it expresses a mechanism in continuous operation, expanding according to definite laws, and adding new units from the central point. That this feature is often curiously missed or miscomprehended, has been well illustrated by D'Arcy Thompson⁴ (1918), who in discussing phyllotaxis-phenomena as presented by Cook,⁵ naively states that he does not see anything mysterious in the mechanism of phyllotaxis, as hinted by the latter writer, beyond simple pattern-building. The most interesting section of this work on 'Growth and Form' is devoted to the exhibition of schemes of transformation as applicable to animal growth-forms; and it is clear that to a zoologist conversant with the growth-increase of an animal to one adult form once, the conception of a 'growing-point', and its wholly mysterious property of continuing to build similar new forms indefinitely, is wholly unfamiliar and unrealized owing to the limitation of the static diagram.

The initial step in any future consideration of Plant-growth, as leading to the initiation of leaf-members at a growing-point is thus the utilization of the geometrical proposition of uniform centric growth about a point; the system being considered in two-dimensional form, as in the transverse plane of a botanical section; since the longitudinal component only adds the factor of linear extension of the system, and such growth-spirals cannot be studied in three dimensions; the effect of the theoretical dome-shaped apex of the plant-shoot being again the expression of secondary phenomena of growth-retardation. That no finite plant-body can be satisfactorily imitated by a mathematical construction expressed in terms of extension to infinity, is sufficiently obvious; but finite propositions may also come later on. The simplest mathematical conception has to be taken first, as satisfying some of the primary features of the problem, but not all: the finite stage of the proposition may be reached in the introduction of *retardation-*

¹ Kepler (1611), cf. Ludwig (1896), 'Weiteres über Fibonacci-Curven', Bot. Centralbl. 68, p. 7.

² Tait, Enc. Brit., ix Edit., vol. 15, p. 723 (Mechanics).

³ Church (1904), Ann. Bot. xviii, p. 227. Fig. I.

⁴ D'Arcy Thompson (1918), 'Growth and Form', p. 639.

⁵ T. A. Cook, 'The Curves of Life', p. 81, 'The Meaning of Spiral Leaf-arrangement'.

effects, which in plant-constructions are associated with the attainment of an adult-form, on the ultimate complete cessation of further growth; the growing system being thus brought to rest.

Leaving on one side all traditional obsessions in favour of postulated cylindrical shoot-systems of adult axes; i.e. omitting longitudinal extension of the system, and taking the two-dimensional expression of the transverse section of a growing-point, it is soon realized that in such a growing bud, the leaf-primordia follow a perfectly straightforward geometrical arrangement, in all normal growing centric systems—expressed in terms of spiral curves, winding and intersecting in opposite senses, the number and ratio of which may be readily checked and scheduled; e.g. in such form as $(m+n)$ or $(m:n)$. The latter, as including the property of orthogonally intersecting log spirals, may be utilized from such a preliminary standpoint, though open to the objection that the curves seen can never be log spirals on any growing plant in which the growth-rate is never mathematically uniform. All phyllotaxis-constructions are thus scheduled in terms of intersecting curves (normal phyllotaxis); such regularity following as a consequence of rhythmic production, i.e. uniform working in the machine: if there is no 'pattern' there is no rhythm, and conversely. The fact that many phyllotaxis-constructions in the plant are so broken, indefinite, and hopeless of interpretation, is thus legitimately regarded as the expression of failure in the mechanism to retain co-ordination; and is to be interpreted biologically as implying decadence of the construction-system; as, for example, in plant-formations in which such systems may be vestigial, and now useless for any practical purpose, and hence the more interesting in their phylogenetic significance. Such cases abound, as, for example, in floral construction (cf. androecium of Poppy, the sporophylls of a large *Clematis*, the pattern of the achenes on a strawberry), or the great bud of *Equisetum Telmateia* with vestigial and rudimentary leaf-teeth.

But however interesting it may be to schedule such numerical factors and their secondary complications, the interpretation of phyllotaxis is concerned with something more; not so much the mere facts of the rhythm, as the causes, still obscure, to which phenomena of rhythm are the response. Thus, in the first place, certain simple generalizations follow from the geometrical relations of such curve-patterns; and these apply to all patterns expressed as lines distributed around a point, whatever the nature of the spiral curves¹: e.g. —

(α) When $m = n$ the construction is *symmetrical*, that is to say, expressed in a complementary system of straight lines and circles. (Fig. IV.)

(β) If m and n are unequal, the construction becomes '*asymmetrical*' or *spiral*, as the most general mathematical case, and is so far to be regarded as 'primitive' in the biological sense, in absence of any reason to the contrary. (Fig. II.)

(γ) In any such asymmetrical construction, lines expressed by sum $(m+n)$ and difference $(m-n)$ of the primary numbers will map out a complementary system, as diagonals of the meshes of the original construction; and other systems, as expressed by continued stages of 'sum and difference', will pass through the same points, with others. The occurrence of summation-series of numbers expressing ratios, has no special relation to the plant, but is the expression of certain general properties of such systems of intersecting curves.

(δ) If m and n have unity only as common factor, one grand spiral will pass through all the points of intersection.

¹ Church (1904). Ann. Bot. xviii, p. 229.

(ε) Where m and n have a common factor (e.g. 2, 3), no one spiral will include all the points; but as many spirals will pass through that part of them as are indicated by the common factor (e.g. two spirals each through half).

(ζ) Where m and n only differ by unity, the grand spiral passing through all the points is conspicuous as the diagonal complementary system.

(θ) The points of intersection, or areas delimited by any such curve-systems, starting from any unit, are readily given a numerical value, or 'numbered up', by the obvious properties of m and n distribution; a simple device (Braun, 1835) which has always proved irresistible to botanical writers, though adding nothing to the original factors of the case, and usually proving very confusing to the beginner, who is apt to take the numbers as unalterable. (Fig. XII.)

It remains to consider to what extent plant-constructions bear out these generalizations; that is to say, supply examples of *all the possible* mathematical cases which may arise; it being so far clear that there is no special virtue or mystery about a spiral curve, except that it may not be so easy to draw as a circle with a compass; all log spirals are in fact curves intermediate between the straight line and the circle; or, preferably, the general expression of a growth-movement of which the straight line and the circle are the limiting cases. Since an absolutely straight line, or a true circle, is inconceivable in a living plasmatic organism, it may be said that all curves in organic nature are based on logarithmic spirals; though again never absolutely attaining to the accuracy of such mathematical conceptions, and liable to a wide range of secondary changes.

On comparing the data given by plant-apices, it is very evident that all the general phenomena of curve-systems are abundantly exemplified, and common examples should be familiar to every botanical student. For example:—

(α) The symmetrical construction is that long known in botany as 'whorled' phyllotaxis, in which members of successive whorls alternate.¹ Superposed symmetrical constructions are exceedingly rare, and do not obtain in any case in which they can be regarded as primitive. All symmetrical systems are again suggestively derivative from earlier conditions of 'spiral' organization; the alternation of the whorls being in fact the strongest evidence in this connexion.

(β) The case of asymmetrical phyllotaxis, in which the numbers have no common factor, is distinctly the most general case; the original recognition of spiral leaf-arrangement is based on this fact.² (Figs. VI, VII.)

(γ) Complementary systems are classed as '*parastichies*' of various grades ('*orthostichies*' also coming under this rule), commonly confusing the analysis of the pattern on the part of earlier writers (cf. 'multiple spirals' of Bonnet): the primary curves of the system may be distinguished as '*contact-parastichies*'.³

(δ) The single grand spiral is in fact the feature commonly appealing to observers of elongated axes, from the times of Bonnet and Schimper; so much so that it has been widely accepted as a causal factor ('*genetic spiral*'); whether rightly or wrongly is still a point at issue.

(ε) The case of the common factor, early recognized by Bravais as the

¹ R.P.M.L., loc. cit., p. 142, 'The Symmetrical Concentrated Type'.

² Leonardo da Vinci, xvi cent., Bonnet, xviii cent.

³ 'Sliding-growth effects' may render the contact-parastichies obscure in older constructions; cp. R.P.M.L., loc. cit., pp. 315, 345.

Bijugate, Trijugate, &c., construction—as a sort of intermediate condition giving both whorls and spirals at the same time, and hence a puzzle—may be sporadic in any line (cf. Pine-cone, *Helianthus capitulum*), but appears characteristic in *Dipsacus* and several *Dipsaceae* (cf. also *Silphium*). In that no single 'genetic spiral' can be postulated for such a construction, it gives the *coup de grâce* to all theories of the causal operation of such a single construction line, and its divergence-angles, in the case of the Flowering Plant.¹

(c) Gives the interesting case of 'spire'-construction; the grand spiral ($m-n$) being complementary to $(m+n)$ more nearly vertical series, and hence presenting as many obvious 'spires' as are expressed by the sum of the construction curves; also sporadic in many series (cf. *Sedum*, *Cyperus*, *Euphorbia biglandulosa*), and following from the (2:3) of the Fibonacci series in 5-spined floral constructions imitating superposed whorls.²

(d) Where higher ratios obtain, the method of numbering up will bring out the contact-relations in the simplest manner; while failure to give connected results in this respect is the criterion of the irregular system and deteriorated mechanism; the latter often local and expressed in varying degree of inaccuracy.

To this may be added as facts of observation:—

(1) The enormous preponderance of Fibonacci numbers in spiral systems, to the extent that any other ratio may be termed relatively rare and exceptional, with the deduction well-warranted that Fibonacci phyllotaxis may be regarded as phylogenetically primitive; while all other constructions are variants, up-grade (symmetrical) or down-grade (irregular).

(2) The fact that Fibonacci numbers are lost in secondary whorled constructions with high numbers, though wonderfully persistent as *distichous* (1+1), *decussate* (2+2), *trimerous* (3+3), symmetry, and curiously vestigial as in the 5 of pentamerous flowers of Dicotyledons, and the 'quincuncial' calyx.

(3) In no case is one number of the ratio more than twice the other ($m:2m$),³ the range being between $m:m$ (whorled) and $m:2m$ (bijugate); these cases are again relatively so few as to be regarded as anomalous, and undoubtedly secondary as 'sports' and 'mutants' of the original mechanism.

(4) Owing to the general effect of the growth-pressures of members in close lateral contact, the theoretical points of intersection are apparently replaced by more or less rhomboidal areas, bounded by parastichy curves, to which all the same generalizations apply. (Fig. VI.)

Given such data it should be possible to recast the whole subject of 'divergence-angles',⁴ in terms of log spiral constructions, to analyse conceptions of the value of bulk-ratio,⁵ or the fact that different shoots of the same plant may produce similar leaf-members in different curve-systems, in correlation with the relative volumes of axis and appendage, and it becomes apparent that older generalizations of the Schimper-Braun type have touched but the fringe of a very remarkable subject; while any ingenious methods involving the acceptance of older Archimedean notations, to be 'corrected' in the process of initiation, or subsequently by secondary 'displacements' of primordia, on the lines indicated by Schwendener, again express a regrettable ignorance of the essential geometry of growth-problems.

¹ R.P.M.L., 'Multijugate Types', p. 166.

² loc. cit., 'Least Concentrated Type', p. 154.

³ loc. cit., p. 342.

⁴ loc. cit., p. 340.

⁵ loc. cit., p. 338.

Undoubtedly the most important point brought out by the examination of shoot-apices in which primordia make their first appearance, is the fact that every form of phyllotaxis-construction which is rhythmic, and works out a pattern, is readily expressed in terms of such intersecting curves, and in no other manner (cf. the bijugate system, and the relation of whorls to spirals). This applies more convincingly to the case of 'rising-phyllotaxis' of the type of *Helianthus* leafy stem and inflorescence; the rules deduced for the latter also explaining the contact-relations of the beautiful bijugate expansion-system of the *Dipsacus*-head, and similarly applicable to more irregular and decadent 'falling' constructions. In all such cases, though it may be possible to trace the single 'genetic spiral' by the method of numbering the units, one can never be wholly convinced that a complex construction has been adjusted and so elegantly fitted together, either by minute changes in 'divergence-angles', or by obscure mechanism of mutual pressure of certain units in the scheme, so much that the system must express the simultaneous growth of a curve-complex, expanding or contracting according to some definite law.¹ (Fig. VIII.)

Similarly all local variations in the original system are readily followed in terms of the addition or loss of the primary parastichy-curves, one at a time, with consequent alteration of the pattern in other respects. For example, a (6:7) construction (cf. Cactaceae), by adding either a 'long curve', or by losing a 'short one', would attain true circular symmetry with whorls as (7:7) and (6:6) respectively; or again by adding a 'short curve' it would appear as (6:8), a bijugate form: in all such cases the original 'genetic spiral'-effect would vanish. Conversely the addition of curves one at a time to a symmetrical system, as in *Casuarina* and *Equisetum*, would give a spiral 'staircase'-effect; though in these highly specialized types the occurrence is so rare as to pass as a 'freak'.

Excessive variations of this type soon lead to hopeless irregularity; and local irregularities wholly destroy any rhythmic effect. In extreme cases one side of a plant may appear normally constructed, and the other be quite irregular and indeterminate.²

Ample evidence is thus at hand that phyllotaxis-mechanism of the shoot-apex is to be referred to an initial choice of curve-systems, comparable with the isolation of equal-spaced lines of growth-potential; and, so far as the Flowering Plant is concerned, is distinctly *not* referable to any single 'genetic spiral', working out as a causal factor the spacing of members at some specially thought out divergence-angle, with the inconceivable accuracy of even seconds of arc in apices commonly only a fraction of a millimetre in diameter. The principle of the log spiral construction based on a view of uniform growth-expansion, in the first instance, merely introduces the conception of growth at some uniform rate, and is the mathematical expression of a centric field of growth involving the expansion of the units as 'similar figures'. Any set of similar figures, whatever their shape will necessarily fall into log spiral lines; and it has been already noted that in plant-constructions the 'similar members' are not absolutely similar, since they are subject to secondary growth-changes, and the 'log-spirals' are never absolute. But assuming a leaf-origin to imply a subsidiary and equally centric disturbance of the primary centric field of growth, it may be legitimate to regard such primordia as essentially *iso-diametric*, and in such case they must bear some relation to simpler *iso-diametric* geometrical units as 'squares' or 'circles'. It is again

¹ R.P.M.L., p. 111, 174.

² loc. cit., p. 97: anomalous head of *Dipsacus*, p. 173.

difficult to distinguish which may be the causal factor and which the consequence.

On the other hand, taking such an interpretation of the growth-expansion scheme as following such equally spaced lines of orthogonal intersection, as most readily drawn quasi-squares, it is easy to pass on to the conception of the quasi-circle; just as with even greater facility the idea of the latter is obtained by merely postulating that *every lateral primordium is initiated from a point as a centric disturbance in a centric growth-system*. The remarkable geometrical attributes of the quasi-circle, as localized in an orthogonally arranged system of such units, have been formulated by Hayes,¹ and the curve itself is defined in such a manner that the initial form of the primordium, referable to any given ratio, as considered in the same two-dimensional transverse section, can be plotted as a standard of reference; as in the expression $(\log \frac{r}{c})^2 + \theta^2 = \frac{\pi^2}{m^2 + n^2}$, (Fig. IX), without prejudice to the fact that such curves will not obtain in any plant in nature; though the approximation may be closer in the higher ratios, and the essentials exist in all, in a secondarily modified form. The special features of these remarkable curves are of the general character noticed in bud-sections, and closer approximation may be readily introduced by adding the effect of a secondary growth-retardation in one or both dimensions.² This fact may be left for future consideration: but so far the geometrical construction and mathematical properties of quasi-circles undoubtedly do afford an illuminative explanation of all the essential and primary attributes of a leaf-appendage accepted by an older school of academic morphologists, contemplating the plant for over a century, in complete ignorance of its phyletic origin in submarine environment, and so far analyzed in text-books as constituting the (1) Bilaterality, (2) Dorsiventrality, (3) Isophylly, of the typical leaf-lamina. That all leaf-primordia necessarily present these essential attributes follows directly from the postulated orthogonal log spiral construction, and not from any other construction. The last point of bilateral symmetry with regard to a radius, in a system otherwise wholly spiral and obliquely asymmetrical, is in fact, the detail which adds the coping-stone to the superstructure of log spiral theory.³

That the reduction of Phyllotaxis-phenomena as presented by subaerial vegetation to a problem of orthogonally intersecting construction-paths, mapping out points of origin for new centres of lateral growth, leaves the subject still an unsolved problem, is sufficiently obvious; but the fact remains that no other conclusion appears possible. No causal factor has been outlined, and in such case it can be only conceded that the construction-scheme may be possibly the expression of an inherited mechanism, or the adaptation of some such scheme of growth-distribution which has been initiated in some previous stage of aquatic existence, as a mechanism older than the vegetation of the land, to be traced back to some more remote horizon of plant-life; though now adapted and improved to suit the more complex conditions of subaerial existence, in further correlation with the increased specialization of the shoot-system of 'axes' and 'appendages'. That is to say, one must be prepared to admit that phyllotaxis-phenomena may be the more modern adaptation of some older construction-mechanism, possibly now working on lines only remotely connected with first origins: and that, as in other biological 'adaptations', the original function,

¹ R.P.M.L., p. 330, 336.

² loc. cit., p. 347.

³ loc. cit., pp. 331, 333.

mechanism, and even working-units, may have been something quite different from what might be concluded from the study of land-vegetation alone. There can be no doubt that abstract conceptions of what a plant ought to be, the expression in text-books of what generations of academic morphologists have evolved from their inner consciousness and the contemplation of land-vegetation alone, have taken very much for granted.

III

ADVANTAGES OF THE EQUIPOTENTIAL THEORY

I. As points in favour of the equipotential theory may be noted :—

(i) It replaces the Archimedean notation of Schimper and Braun, well-known in the form of 'divergence-fractions', clearly incapable of expressing the construction of a growing apex (and never intended to do so), by a construction in terms of growing spirals. That is to say, it replaces an obviously *false* notation by a more *correct* one. The notation employed merely expresses the simple facts of observation, about which there can be no dispute, in a form which is also mathematically innocuous; i. e. so many paths cross so many, of the form $(m+n)$. The use of a ratio $(m:n)$ or (m/n) , which would definitely imply a system of orthogonally intersecting log spirals should be avoided, since the intersections actually observed on a plant are not orthogonal, and, as already pointed out, can never be regarded as such. The crossing is a fact of observation; the ratio is a matter of mathematical theory. At the same time, it is not to be denied that ratio-formulae will be probably utilized in the future.

(ii) The principles of orthogonal construction lead directly to the enunciation of the quasi-circle as the fundamental plane-representation of all lateral primordia, which involve circular fields of growth contained within a parent circular field; while corresponding systems of quasi-squares may afford convenient representations of primordia in close lateral contact. Such systems constitute a valuable *Standard of Reference* for dealing with the properties and forms of such primordia, however little they may be like them at first sight. The increasing resemblance of such figures to the transverse sections of leaf-members, when secondarily modified by packing and growth-retardation, will be considered later.

(iii) The quasi-circle hypothesis in turn elucidates the remarkable properties of leaf-members, their *bilaterality*, *dorsiventrality*, and also the essential *isophylly* (otherwise inexplicable) of the lamina in spiral as well as in whorled constructions, as a purely mathematical deduction; but it at once renders other points clear, and in a manner which was not previously considered. In the last case it emphasizes a remarkable property of leaf-form, so accepted as a commonplace, that it had never attracted any special notice; though attention has been paid to the interpretation (usually teleological) of anisophylly.

(iv) It again renders great service in clearing up the difficulty of the 'slipping' of the members of spiral systems which formed so prominent a feature in Schwendener's 'Contact-Pressure Theory'. Since the primordia of a spiral system are bilaterally symmetrical with regard to a radius of the whole system so long as they are free from one another, while under contact-pressure they tend to be squeezed into the asymmetrical meshes of a packed spiral pattern; the 'slip' of the free portion of the member

as it escapes its neighbours thus tends to make it recover its original radially symmetrical relations with regard to the main axis; so that, in the limit, its *tangential* diameter becomes again a circular path of the main system, instead of a spiral path in the packed system. This simple solution of the Schwendenerian 'slip', which may be plotted geometrically, at once puts the contact-pressure theory out of court; quite apart from the fact that Schwendener, in postulating circular primordia in orthogonal series, had laid the foundation of the equipotential theory, if he had not been lost in helical constructions.

(v) The most interesting application of the theory undoubtedly lies in the manner in which it amplifies the conclusions of Wiesner on the principle of the maximum illumination of the members of a leafy shoot. As shown by Wiesner, many years ago, the most plausible interpretation of the occurrence of numbers belonging to the Fibonacci-series in the plant-kingdom, is that they are associated with the geometry of space-distribution, and involve a divergence-angle which will promote maximum illumination of the overlapping series of members. The standpoint was not entirely new, since Bonnet, the pioneer of spiral construction, gave as the 'final cause' of spiral phyllotaxis the biological standpoint that '*Transpiration which takes place in the leaves demands that air should circulate freely around them, and that they should overlap as little as possible*'; thus giving from the first the conception of the advantage of minimum superposition. This was obviously in accordance with the physiological ideas of the time, when the nutrition of plants was considered as effected solely by the absorption of substances from the soil by means of the roots. After Sachs had successfully demonstrated the essentials of photosynthesis (1865), it became possible for Wiesner to restate the problem in terms of light (1875). But the two standpoints still remain intermingled, when it is remembered that exposure to light, by promoting excessive transpiration (chloro-evaporation), may soon reach a point at which the emission of water-vapour may overpass the limit of the root-supply, and xerophytic conditions may obtain. Thus maximum superposition may be advantageous at one period, but directly injurious at another, and the plant has to effect some sort of compromise. Hence phyllotaxis-relations are intimately associated with conditions of both maximum and minimum superposition; it is a mistake to keep one's attention too fixed on the former standpoint alone. Wiesner showed that for all series of phyllotaxis-fractions, the one involving Fibonacci numbers gave the most equal distribution on the axis for a given number of leaves. That equal balancing of the leafy shoot, which is admirably attained by all whorled systems, is not the essential feature, was also claimed by Wiesner (1902);¹ and the mathematical deduction holds,

that for a given number of leaves a divergence of $\frac{3-\sqrt{5}}{2}$ of 360° would give minimum superposition, while $\frac{1}{2}$ of 360° gives the maximum. These deductions of Wiesner were purely mathematical, and were based on the familiar series of fractional divergences of Schimper— $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, &c., &c.,

expressed as values of the continued fraction $\frac{1}{x + \frac{1}{1 + \frac{1}{1 + \frac{1}{\dots}}}}$ To suit this series

x was taken as = 1, and the limiting angle $\frac{\sqrt{5}-1}{2}$ of $360^\circ = 222^\circ 29' 32''$.

¹ Wiesner (1875), Flora, 58, p. 113, 'Bemerkungen über rationale und irrationale Divergenzen'; (1902), Berichte, 20, p. 84, 'Über die Beziehungen der Stellungsverhältnisse der Laubblätter zur Beleuchtung'.

The result would be written more conveniently as the inverse angle, with $x = 2$, since the ratios $\frac{1}{2}$, $\frac{2}{3}$, $\frac{3}{5}$, $\frac{5}{8}$, &c., are complementary to the preceding, in which case the limiting angle = $\frac{3-\sqrt{5}}{2}$ of $360^\circ = 137^\circ 30' 28.936''$ (Bravais), the familiar 'Ideal Angle' of Schimper. This angle, which has so long persisted as a somewhat mystical conception, has been always repugnant to a number of botanists, to whom the 'progression towards perfection' implied by a rise in the phyllotaxis-fraction appeared wholly unreasonable, from the standpoint that the majority of leafy shoots are expressed in low divergences; and there is no evidence whatever that the highest divergence known (cf. disk-florets of *Helianthus*, as compared with foliage-leaves of the stem) has anything to do with a more perfect perception of illumination. In his later paper (1903) Wiesner still remains handicapped by this retention of the helical constructions of Schimper and Braun, which again were mathematical expressions, and not simple data obtained from the plant itself. For example, it is abundantly clear that if the divergence angle of $137^\circ 30' 28.936''$ is the Ideal Angle for maximum illumination, the plant-shoot which is so commonly classed as a ' $\frac{2}{5}$ ' construction, with a divergence-angle of 144° , is so far removed from the optimum, that one hesitates to see the particular advantage of the mechanism which can allow such a constant error in the angle.

Once the subject is freed from the obsessions of these helical divergence-angles, which have no connexion with a growing-apex, it is interesting to compare the results given by the assumption of orthogonal construction.

Thus the systems become:—

I. *On adult shoot with equal internodes.*

$$\begin{aligned} \frac{2}{5} \text{ of } 360^\circ &= 144^\circ. \\ \frac{3}{8} \text{ of } 360^\circ &= 135^\circ. \\ \frac{5}{13} \text{ of } 360^\circ &= 138^\circ 27' 41.54''. \end{aligned}$$

II. *At the growing-point.*

$$\begin{aligned} (2+3) &= 138^\circ 27' 42''. \\ (3+5) &= 137^\circ 38' 50''. \\ (5+8) &= 137^\circ 31' 41''. \end{aligned}$$

These figures suffice to show that the optimum angle may be actually attained within one degree for the (2+3) system; while at (5+8) (cf. *Pinus*, *Aspidium*, *Helianthus*) it may be attained within almost *one minute*; if, that is to say, the mechanism the plant has at its disposal for building the system be sufficiently accurate. Apart from mathematical accuracy, it may be said that the plant-constructions indicated by these formulae may really attain the postulated angle with an accuracy sufficient for all practical purposes, or what is equally important, as near as we can measure it, as well in the lower systems as in the higher. Such a conclusion again brings Wiesner's generalization immediately within practical range. There can be no doubt as to the correctness of his standpoint; but the log spiral theory is needed before the argument can be regarded as finally established; and it can so far be definitely stated that the angle $\frac{3-\sqrt{5}}{2}$ of 360° , the 'Ideal Angle', is no longer a mystical conception of *aim* on the part of the plant, but, within the range of one degree, an actual mathematical property of Fibonacci phyllotaxis for all ratios of (2+3) and upwards. The fact remains that Wiesner formulated these principles with imperfect mathematical data; with corrected figures they are plain to any one; at any rate so far as the significance of the Fibonacci numerals in plant-construction is concerned.

From the fact that Fibonacci phyllotaxis gives optimum illumination to a vertically adjusted leafy shoot, it follows that any deviation from Fibonacci systems, either as 'anomalous' or whorled constructions, implies

a definite diminution of exposure,¹ which may be utilized as a 'xerophytic adaptation'; and as a matter of fact such constructions are, on the whole, characteristic of xeromorphic vegetation, though by no means invariably so. On the other hand it is equally important to remember that direct formation of a more or less overlapping pattern is but one means out of many by which the plant is able to control its light-supply. In internodal extension, petiole-formation, leaf-dissection, diminution of surface, erection, drooping, petiolar torsion, &c., &c., we have to do with a whole series of mechanisms which correct or adjust the exposure of the leaf-lamina, whatever may be the initial pattern as built at the growing-point of the shoot. A pattern, the construction-factors of which may be hereditary and settled at a relatively distant point in the phylogeny of the race, may receive subsequent *compensatory adjustments*; that is to say, the mutation which marks a new and successful adjustment does not necessarily involve the initial pattern at all, but may be something wholly different. A change of pattern represents only one possibility out of many, and these probably in the long run even more effective. Plants with perfect Fibonacci systems may be secondarily adapted for extreme xerophytic conditions (cf. rosettes of *Sempervivum*, reduced needle-leaves of *Araucaria excelsa*), just as others with systems presenting minimum exposure may be secondarily adjusted for diffuse light. Similarly, while the vegetative part of a plant may present a system with considerable overlapping (decussate 2 + 2), the floral axis involving purely non-assimilatory members may revert to the primary Fibonacci pattern (cf. *Calycanthus*, foliage (2 + 2), flower (5 + 8) throughout). In fact the paradox remains, so manifold and so complex are the secondary compensations of the initial scheme, that the most perfect examples of purely 'mechanical' phyllotaxis-patterns only survive in shoot-systems which do not include leaf-members devoted to photosynthesis at all. Hence the scales of the Pine-cone, the disk-florets of *Helianthus* and other Composites, the spines of leafless Cacti, and the bractless florets of *Arnica*, afford at the present day the most classical expressions of spiral patterns which are inherited and accurately followed; since, though now entirely useless from their primary significance, they retain their essential character as equally balanced constructions. Similarly the best-established case of a change of the phyllotaxis-pattern under the direct effect of illumination is to be seen in a plant which has no leaves at all (*Cereus*).

So involved are the general phenomena of leaf-arrangement that a few common examples may be utilized to exemplify the fact that Wiesner's Law would be of phylogenetic rather than of ontogenetic significance; while the relation of the system to the water-problem may be as vital as its requirements of light for photosynthesis.

Thus (1) the common Ivy (*Hedera*), which produces strong and erect shoots in normal Fibonacci (2 + 3) series, in the condition for maximum illumination, also bears reduced (1 + 1) running shoots in the construction for minimum illumination (this being constant for some varieties, e.g. erect shoots of *H. helix*, var. *arborescens*). The (2 + 3) condition is evidently the primitive form, and is associated with the pentamerous floral construction; but the mutation to (1 + 1) is not necessarily a success: when growing against a surface, with unilateral illumination, both systems are almost equally unsuitable and require to be compensated by (1) extensive production of internodes, (2) petiolar torsion. The (1 + 1) system clearly owes its origin to a reduction-process involving fewer leaves and reduced transpiration.

(2) Foliage-shoots of *Fuchsia gracilis* are sent up from plants cut back by frost in construction-systems of (2 + 2), (3 + 3), (4 + 4), and more rarely (2 + 3).

¹ Wiesner (1902), loc. cit., p. (97); (1903), 'Zur Biologie der Blattstellung', Biol. Centralbl., 23, p. 209.

The leaves are small, well-spaced apart on relatively long internodes, and all appear equally suitable for photosynthesis, so far as can be judged by the eye; yet one is bound to assume that the less frequent $(2+3)$ Fibonacci system is the primitive one for the species, not merely from the fact that one may be biased in favour of the system, but that the tetramerous flowers of *Fuchsia* are undoubtedly reduced from corresponding pentamerous ones; and these in turn must have had the familiar quincuncial calyx which is the Fibonacci construction. It is further clear that while $(2+2)$ is now the normal type for the assimilatory shoots, the systems $(3+3)$ and $(4+4)$ occur as amplifications, due to increased vigour in shoot-production; the method of superposition is not altered, but the number of leaves is increased, giving greater activity to transpiration and photosynthesis.

(3) The well-known case of seedlings of *Cereus* and *Phyllocactus* affords examples of such constructions as $(2+2) = 4$ -ridged, $(2+3) = 5$ -ridged, and $(3+3) = 6$ -ridged plants, the ridges being developed along the orthostichy lines. On exposure to strong light the cladodes change to 3-ridged $= (1+2)$ and 2-ridged $= (1+1)$ systems.¹ The phyllotaxis construction of these leafless plants is thus modified to suit the production of 3- or 2-angled cladodes. Such a case of direct modification is almost inconceivable in the case of a leafy shoot in which compensatory adjustments may be more readily effected in the case of members and structures already in existence. In a leafless Cactus the only alternative is a simple cladode-flattening which need not involve the phyllotaxis-system at all; and this occurs noticeably in *Opuntia*, the original phyllotaxis pattern straggling over the flattened laminae. Nor can the case of *Phyllocactus* be regarded as solely due to the direct effect of light. Strong plants of *Cereus*, pruned hard back to the bare stems, similarly send up an abundance of new young shoots in the same construction-systems, and these again, as they grow old, change into 3- and 2-ridged laminae in just the same way, when growing all the time under constant conditions of illumination. It is increasingly evident that the water-supply is the essential factor, and the apparent effect of light is due to the greatly enhanced chloro-evaporation. In such cases the phenomena are of the nature of reduction-phenomena as xerophytic adaptations in a starved apex.² It is much easier to understand the direct effect of want of water, or diminished supply, in the growing apex, than to postulate a mechanism for light-perception in the assimilatory regions which may be conducted to the growing-centre at which the pattern is being initiated. In these shoots also it is evident that the $(2+3)$ system, which is associated with the general tendency to retain Fibonacci systems in the construction of the floral perianth, is to be regarded as the phylogenetically older system; in which case the $(2+2)$ and the $(3+3)$ shoots appear as the nearest simple variants on the pattern, both equally likely to occur in the case of a plant to which the mechanism of minimum superposition is no longer essential.

Equally interesting in this connexion is the case of *Eucalyptus*, the Blue Gum: with the supersession of the decussating blue 'juvenile leaves' by the more xerophytic drooping 'scimitar leaves', the ancestral $(2+3)$ Fibonacci system is either immediately or very soon regained: this may be taken as indicating that the decussate arrangement of the juvenile leaves is really a relic of an older adaptation in the special condition of the seedling.

(4) Lastly, when expressed in low ratios, it is interesting to note how small an alteration (in the form of a 'mutation') may change the phyllotaxis-system from a position of maximum to that of practically minimum exposure. Thus the $(2+2)$ system affords, on the whole, the most general example of a superposed system utilized by xerophytic plants; yet the mere addition of one new

¹ Vöchting (1894), Prings. Jahrb., xxvi, p. 438.

² Molisch (1912), Sitzungsberichte k. Akad. Wien, p. 833, gives a similar case in which three hours' exposure to radium emanation induced a deteriorated effect in apices of *Sedum Sieboldii*, a $(3+3)$ construction 'reducing' to $(2+2)$, as usual in starved shoots.

path renders it (2 + 3) with all the advantages of the Fibonacci ratio. Similarly another new path, by changing it to (3 + 3), gives again another case of practical superposition. All three examples occur in the flowers of *Herbertis vulgaris*, and again in the inflorescences of *B. aquifolium*, in which cases they can have no special significance from the standpoint of light, but are merely accidents of construction; useful only to point the moral of the readiness with which non-essential phyllotaxis-constants may undergo modification, and the fact that simple numerical factors may be alone variable in a construction which involves a complex mechanism.

So far, then, Wiesner's Law is the best teleological expression of the demand for maximum illumination, and may be provisionally regarded as indicating the 'aim' of the land-plant under favourable conditions of light and water-supply. But maximum illumination may soon become injurious: (1) from the direct effect of intense light; (2) from induced excessive transpiration. In the case of the former, superposition will give protection from light-injury, in the latter it will give also protection from desiccation. Hence reduced superposed systems become characteristic xerophytic adaptations, and the ultimate cases, the decussate (2 + 2) and the distichous (1 + 1), occur as very general limiting phenomena of shoot-construction. The intermediate (1 + 2) is less easy to check when the number of leaves is few; when they are closely packed this system is also commonly compensated by 'torsion', as in *Apicra spiralis*, *Cyperus alternifolius*, and *Pandanus*.¹

In conclusion, it would appear that Wiesner's generalization is to be taken only in its widest significance as a general law for land-vegetation, dating far back in the phylogeny of the race, and hence so deeply ingrained that it is not lightly changed. Individual apparent exceptions and special cases cannot be considered merely on their merits, without knowing something of their phylogenetic history. Thus whatever be the phyllotaxis of the vegetative system, the existence of trimerous and pentamerous flowers, and more particularly the latter, all point to the universality of the Fibonacci type of phyllotaxis in the parent stock of Modern Plants, apparently as the solution of the problem of maximum illumination. The ancestral forms of all these last special cases must have been originally endowed with Fibonacci phyllotaxis in the vegetative shoot, however much it may have been modified since. The general problem will be to account for this phylogenetic feature. It is also evident that, in approaching the subject of the mechanism of phyllotaxis-systems, the Fibonacci ratios are of primary importance; all other types of construction being regarded as derivatives of this parent form.

It may be objected that here, as in other purely teleological interpretations, Wiesner's theory seeks to prove too much. In thus exalting the virtues of the Fibonacci ratios under maximum illumination by vertical light, it has little to say on the relative value of other constructions, closely similar at first sight (anomalous and bijugate systems), and often characteristic of plants by no means badly illuminated (*Dipsacus*, *Cephalaria*, *Silphium*). Nor can a whorled (decussate) construction be shown to be objectionable in any known case (*Acer*, *Fraxinus*, *Aesculus*) of shoots with no marked xerophytic tendency. All compensatory effects avoid any change in the construction-system at the actual apex. Nor is it clear how any growing-point could become conscious of the fact that its arrangements were ultimately unsatisfactory, or know how to alter them, or what would be the correct solution of the problem! Compensatory growth-effects and xerophytic adaptations are put in where the requisite mechanism is available, as implying tissue-differentiation in Zone III, or intercalary extensions in

¹ R.P.M.L., p. 159.

Zone II, but never any change in the minute growing-point (Zone I). Nor, again, is vertical light such an essential consideration; the vast majority of plant-shoots are lateral and axillary, obliquely illuminated at their first inception, if at all; yet no distinction can be drawn between the apical construction of terminals and laterals. In a few examples noted (*Silphium*, *Dipsacus*) the terminals are bijugate and the laterals present the pure Fibonacci organization. Nor can any such considerations apply to the entire range of the complex subject of floral-phyllotaxis. The fact that the individual never 'corrects' the phyllotaxis-construction of its apex, whatever the external illumination, goes to show that teleological interpretations applying to the ontogeny of the individual are meaningless; and though it may be more plausible to regard such agencies as effective in the *phylogeny* of the race, there is little evidence, so far as land-plants are concerned, of any mechanism which might so respond to conditions of illumination, any more than it does at the present time. One has to fall back on the effect of natural selection acting on chance *mutations* in the construction-system; and though it is quite possible and indeed general for plants with Fibonacci phyllotaxis to deteriorate such construction in every possible manner (to whorled, anomalous, bijugate, and wholly irregular constructions), there is nothing whatever to show how it may be possible for the happy solution of the Fibonacci angle and ratio, with its remarkable properties, ever to arise as a chance mutation.

IV

OBJECTIONS TO THE EQUIPOTENTIAL THEORY

ON the other hand, objections to the equipotential theory, as given in precise mathematical form, occur naturally to the botanist:—

(i) If constructions, as postulated in terms of infinite log spiral curves, are equally by theory impossible in the case of a plant presenting only finite growth,—To what extent can the angles calculated from them, or from any other data, be regarded as quite reliable; or to what extent may they be accepted as mere approximations? It is sufficiently evident that the rate of active growth of primordia at the apex of a plant-shoot slows down as the adult stage is reached; and such retardation is the necessary accompaniment of plant-construction. The examination of such retardation should thus have an important bearing on the general phenomena of phyllotaxis. For example:—As the entire systems are considered primarily from the standpoint of the transverse component of the apex, it is evident that such retardation may be analysed into (1) retardation along the radial paths of the section, and (2) retardation along the tangential paths. Consideration of these factors separately shows at once that no radial retardation can affect the angular divergences between members; since variation in growth along the radial paths leaves the primordia still travelling outwards along the same radii as before, but at slower rates. On the other hand, any retardation along the tangential circular paths merely pulls the surface over in the form of the dome-shaped apex which is the familiar accompaniment of shoot-development; and as the transverse plane is alone considered, this part of the retardation-effect vanishes so far as present purposes are concerned. In all such systems, however the growth be modified, the *angular divergence remains unaffected*, since each

primordium travels radially along its own path. This is the essence of the quasi-circle hypothesis; in that it eliminates at once all mysterious conceptions of 'Spiral growth', or 'Spiral movement', at the apex of a plant. A spiral pattern does not imply spiral movement; the direction of growth is purely radial; the spiral curves of the pattern being merely retained as the system expands. The angles calculated for log spiral data are thus the true divergence-angles of all centric phyllotaxis systems; and the tabulated series at once shows how perfect may be the approximation to the Ideal Angle. So close is the approximation, that there can be little doubt as to the suggestive value of Wiesner's Law, and that spiral phyllotaxis in terms of Fibonacci ratios has been acquired phylogenetically, and not ontogenetically, in each individual case, in direct response to the problem of maximum light-supply: just as, on the other hand, symmetrical whorled construction, or any deviation from the Fibonacci Law, tends to approximate the solution of the converse problem of minimum illumination, which is quite as important in the case of vegetation periodically exposed to intense light.

(ii) The next most important objection is the difficulty of establishing the actual means whereby such mathematical relations may be effected in the growing-point of a stem, in what may be regarded (omitting the cell-walls) as a fairly homogeneous multinucleate mass of protoplasm. The problem of energy-distribution in such an apex, only suggested by the theory, still remains extremely vague; yet what can be said on the subject may be briefly discussed later. At the present stage it is not immaterial to point out that the physical, ionic, and molecular relations of a growing mass of protoplasm probably represent the most infinitely complex construction in nature, and any facts which tend to throw light on it beyond the range of visibility should be welcome. At any rate the problem of the ontogeny of a phyllotaxis-construction must be approached sooner or later: the present suggestion merely ceases at the point that it can be only referred to manifestations of molecular forces.

(iii) Apart from the actual ontogeny of the members at a growing-point in the rhythmic sequence denoted by a phyllotaxis-system, further problems are involved in the initiation of the systems themselves; whether

(1) at the apex of a seedling.

(2) at the growing-point of a lateral branch.

(3) the initiation *de novo* on a cell-surface, as on the leaves of *Asplenium bulbiferum*, *Nymphaea* sp.

This section of the subject comprises not only the initiation of whorled and spiral constructions, but also the *orientation* of these systems with regard to the parent axis. Questions of the initiation and orientation of lateral axes have been very largely dominated by views of contact-pressure from Schwendener (1875) to van Iterson (1907), (cf. Weisse in Goebel's Organography, 1900, Eng. Trans., p. 82), even when such hypotheses have been recognized as worthless in affording any explanation of the constructions at the main apices: this being largely due to the fact that in so many familiar cases of axillary bud-development the young members appear to arise in such confined quarters that the influence of the pressure of adjacent appendages is sufficiently suggestive to the eye. Among the many difficulties of such a view may be mentioned:—

(1) The actual initiation of new centres, which must take place before any growth-effect can be seen as 'leaf-primordia', does not demand any obviously clear space. Axillary buds which develop in positions in which contact-pressure may be wholly wanting, as on rapidly extending shoots of *Passiflora* and *Cobaea*, present constructions which differ in no respect from those of the most closely compacted buds.

(2) Identical contact-relations are not followed by similar result. Thus, in lateral branches of *Araucaria excelsa*, lateral buds arise in the axils of certain leaves of a system (8 + 13), giving two lateral orthostichies of lateral branches in a frondose form. The contact-conditions are identical for every bud on either side of the main shoot, yet the bud-constructions are R. and L. image-patterns without rule. (Fig. XI).

(3) Theories of contact-pressure ignore the remarkable phyllotaxis-constructions characteristic of the ontogeny of flower-buds. The fact that the vast majority of floral shoots are orientated with the fourth member, or sepal 2 of the quincuncial calyx, 'median posterior,' shows that some positions may become constants, with possibly subsequent biological benefit. Yet, (a) the Papilionaceae retain sepal 1 (the third member) median anterior with great reliability; (b) the twin-image patterns (R. and L.) are very approximately equally distributed, apart from the phenomena of dichasial construction; (c) while the majority of flowers have sepal 2 'median posterior', others (cf. *Lobelia*) present the inverted twin-image (sepal 2, anterior) with equal constancy, under apparently identical conditions of origin.

(iv) The next most important question concerns the conceivable phylogeny of the mechanism. This difficulty, again, must be approached sooner or later: the present paper concludes with a few remarks on the more obvious features of the problem; more particularly as affecting the relation of the equipotential theory to 'Land Flora', and the general features of other systems of space-form and ramification which do not come under the same ideas of mechanism.

(v) Lastly may be mentioned the most serious objection, common to all mathematical considerations of phyllotaxis-problems, and the one which appeals most directly to every botanist, not so much to those with a distaste for exact figures, as to those possessing a healthy scepticism, in dealing with plant-protoplasm, as to whether it is ever possible for a plant to work in any precise mathematical manner which can be readily formulated. This has been admirably expressed by Sachs as the error of 'gratuitously introduced mathematics'. In fact, why introduce mathematics at all? To what extent do any mathematical relations whatever exist in the plant? and to what extent is the introduction of mathematical calculations or theory to be justified, either from the standpoint of descriptive morphology, the actual physiological mechanism of production, or the utility of the schemes in biology.

The classical generalizations associated with the names of Schimper and Braun, divested of all extraneous theoretical deductions, reduce to the very elementary fact that, on looking round the plant-kingdom, as a matter of simple observation, the great majority of plant-shoots show a remarkable tendency to the repetition of certain numbers, as seen on counting the patterns in which the leaf-systems are expressed. The most frequent of these numbers, put down on paper in numerical order, may be written 1, 2, 3, 5, 8, 13, 21, and the series may be extended to 34, 55, 89, 144, in less frequent examples, but no further. This is a fact of botanical observation; and when to this is added the fact that the contact-parastichies are always indicated by a successive pair of these numbers, it is legitimate to deduce the conclusion that it is the peculiar ratio (approximately constant) indicated by these Fibonacci numbers, which is the essential point of the whole story. This is all that the numbers give, and all that is required for Wiesner's Law. The superposed edifice of 'Ideal angles', 'Other series', 'Complementary series', 'Divergence angles', 'Fractional expressions', 'Orthostichies', &c., are so much mathematical elaboration, more or less purely irrelevant, which adds nothing whatever to the simple facts contributed by the plant; and, as we have seen, such mathematical 'playing with figures', as Sachs

termed it, soon went entirely off the track with the interposition of the helical constructions, originated by Calandrini (1754), which cannot depict in any sense the facts of ontogeny at a growing-apex. In the same way, even Wiesner's hypothesis was originally established as a mathematical proposition solely on these mathematically deduced fractions. The general law follows readily from the properties of the Fibonacci series, but the method of approaching it through the discussion of continued fractions, which can have no bearing on the plant, rendered it obscure; especially so, as Wiesner (1875) was pleased to show by this means that the 'Main series' of divergence-fractions would be more advantageous than any other series for purposes of minimum overlapping. The 'Other series' are purely imaginary conceptions, built up along absurd idealistic lines of thought, many of which are still to be found in text-books.¹ Similarly the log spiral notation, although going back to simple numerals, is at first sight rendered so complicated by the addition of little-known spiral constructions, that it only adds further difficulty to a bewildering mass of figures. The new 'divergence angles' rather add to the confusion than otherwise. For example, did any botanist in his senses ever believe that the scales of a Pine-cone, with a phyllotaxis expressed in the books as $\frac{1}{2}$, are actually, or were ever really laid down at a divergence-angle of $\frac{1}{2}$ of $360^\circ = 137^\circ 8' 34.28''$ from one another; the cone being obviously not a cylinder, and the orthostichies not straight; or is it made much clearer by saying that the (8 + 13) cone has its scales really at a divergence of $137^\circ 30' 38''$.² Yet if they were not, what is the good of introducing the theory? Or, again, do we believe that the disk-florets of a ' $\frac{1}{2}$ ' Sunflower-head were laid down at a divergence angle of $137^\circ 31' 41.12''$, while those of a ' $\frac{4}{13}$ ' head were accurate to $137^\circ 30'$?³ Can we even form a mental picture of the accuracy of such angles, or do we stop to think what is meant by one minute of arc in the case of a small circle?⁴ On the other hand, as already indicated, if $137^\circ 30' 28.936''$ is the ideal angle for exposing a given number of leaves for purposes of photosynthesis, accurate to seconds and a number of decimal places, why are so many plants satisfied with a ' $\frac{1}{2}$ ' system of 144° exactly. Again, taking log spiral notation, is it to be supposed that the leaves of a (2 + 3) system are instead accurately spaced at $138^\circ 27' 42''$,⁵ as already suggested? Are these things accurately true? or if not, to what extent may they be approximately true, or be considered as true within reasonable range, and what is reasonable range? Before any advance in phyllotaxis-theory can be made, these questions require to be answered and placed on a sound footing. If our conceptions of phyllotaxis are now given as based on orthogonally intersecting log spirals, and it has been admitted that—

- (1) log spirals never occur in any plant;
- (2) the orthogonal construction can never be measured, and is not supposed to obtain;
- (3) if the postulated divergence-angles are not true either, or cannot be measured; the whole subject appears so hopelessly futile, that one wonders why it was ever put forward, or what any one could have ever seen in it.

However, the object of the present paper is to show that the Equipotential

¹ Van Tieghem (1891), 'Traité de Botanique', p. 55: Sachs, Text-book, p. 181.

² R.P.M.L., p. 340.

³ R.P.M.L., p. 6.

⁴ For example, on a plant-apex 1 mm. diam., the 10 μ nuclei of the peripheral cells would subtend an angle of more than one degree! One cell-end of apical meristem in a smaller growing-point may easily subtend 5-10 degrees. Hence mathematical discussions in terms of minutes and seconds can be generally ignored.

⁵ R.P.M.L., p. 340.

Theory has sufficient evidence in its favour to survive all these destructive criticisms, since it is itself a constructive hypothesis. Its value consists in affording a *first step* in a subject which so rapidly increases in complexity that without such a guiding conception the problem could never be disentangled. To take a simple illustration:—An ordinary tree-trunk with cambial increase, adding a ring of wood every year, can be considered as working out a series of concentric circles, and the original pith should remain the centre of the circumference indicated by the old trunk. This is a simple geometrical conception; but no botanist supposes that any old tree-stem cut across would ever yield a mathematically exact circle, or that the pith would ever be in the geometrical centre. One might be pleased to find a specimen approximating a system of concentric circles to illustrate an elementary lecture, but that is all. On the other hand, what happens is this:—the simple geometrical conception remains as a standard of reference, useful enough in its way, and following from simple premisses. It is clear that if these premisses alone were concerned, the plant would work on the postulated geometrical form; but the problem becomes increasingly complicated by secondary factors: the value of the standard of reference, however, remains unaffected. The Equipotential Theory has been put forward primarily as such a *Standard of Reference*, in dealing with phyllotaxis-constructions as seen in transverse sections of the growing-points of plant-shoots. The mathematical consequences of such systems have been deduced and tabulated definitely from a mathematical standpoint: evidences have been obtained from plant-constructions which suggested that such a course was justifiable and worth doing. After all, we do have Fibonacci numbers (among others); we do have spiral patterns, and a growing system; these phenomena require to be explained. However, as previously indicated, the point at which the ordinary botanist hesitates is the marvellous precision of the so-called 'divergence angles' to several places of decimals of a second, which are all deduced mathematically, and not measured on the plant at all. This may give an aspect of pseudo-scientific accuracy to the text-book presentation of the subject, but are these things really so? Is the plant accurate or not; to what extent are we justified in demanding scientific accuracy, which may be non-existent.

The standpoint taken up here is sufficiently straightforward. *One is not justified in assuming any accuracy in the plant whatever, beyond what can be measured*, or fairly assumed, as in the case illustrated by the circular tree-trunk. Deductions for practical purposes (e.g. to illustrate Wiesner's Law) must be taken from actual plant-specimens. A living plant is preferable to Wiesner's models of photographic paper set at angles only roughly approximated by hand. Calculations involving minutes and seconds are useless when it is difficult to guarantee accuracy to several degrees. However much mathematical conclusions are useful and suggestive as a standard of reference to keep by one, there is no justification for going beyond data actually obtained from plants themselves. Preferably the matter may be made clearer by keeping the mathematical data strictly on one side, and the plant-data on the other. What exactly does the plant give, and what questions are to be looked up on the mathematical side? To do this a method is required; and again it is in establishing such a method that the utility of the Equipotential Theory becomes at once apparent, as affording the essential standard of reference, which serves not only as guide to the mode of operation, but suggests the working-methods to be employed. Nor is this merely 'seeing in the plant-apex what we want to see'. The proof of the utility of a theory is found in the fact that it serves to bring out points which would otherwise have escaped observation.

GENERAL METHOD FOR THE EXAMINATION OF PHYLLOTAXIS-PHENOMENA

IF all mathematical data are merely mathematical generalizations, useful as a Standard of Reference, but never directly obtained from the plant; if orthostichy lines are merely properties of systems of spirals of Archimedes, which only obtain with members of equal volume or equal radial depths; if intersecting contact-parastichies can be only traced in a few standard examples, as for instance the Pine-cone, in which practically no secondary compensatory disturbances have affected the original pattern,—it remains to consider to what extent it may be possible to obtain any really reliable method for dealing with actual plant-constructions. It is so far obvious that the growing-point at which the system is 'laid down', and just becomes visible, is the only region concerned. Whatever secondary influences come into operation, and however invisible the first causes, it is not possible to go behind the first appearance of the primordia themselves on the actual arched or flat growing-point surface; while this region can be only dealt with, to any degree of accuracy, by carefully cut sections. It remains, therefore, to obtain a fairly satisfactory method for the examination of an actual apical system. For this purpose a fairly large bud-apex, with well-marked simple leaf-primordia and little longitudinal extension in the main axis, is to be preferred. Sections of hardened spirit-material, cut by hand, are subsequently treated with potash and Eau de Javelle to counteract distortion and bring the object, as near as possible, to the normal condition.

A drawing of such a section, grazing the smooth apex of the growing-point in *Sempervivum calcaratum* is given in Fig. XII. On an ordinary pencil drawing, the original figure being 7–8 inches in diameter (Zeiss, A., Oc. 3, Cam. Lucid.), angles can be measured to half a degree, and linear dimensions to half a millimetre. Of the various errors likely to be introduced, the most important are: (1) shrinkage-effects in the material; (2) the difficulty of keeping the section exactly transverse; (3) the difficulty of estimating the exact centre of the system.

The figure illustrates a broad circular apex producing rounded primordia which pass over into areas with rhomboidal section: 30 members are more or less fully shown; and these, on being numbered up, indicate that the system would be defined as a (3+5) construction, and would be imitated by utilizing a curve-tracing of the form obtained by drawing a line through 3–5–8–11–14–17–12–7–2. There is nothing particularly remarkable about the section, or about the manner in which it is obtained: shrinkage-effects are obvious: in several cases the leaf-primordia are widely spaced (3–4 mm.), and yet show parallel curves. Such extensive shrinkage will introduce so considerable an error, when calculations are made to half a millimetre, that further accuracy of measurement is needless. There is no means of ascertaining the exact centre of the apex, within a millimetre at least; and the error from this will be again considerable. Similarly the difficulty of keeping the section level, or at right angles to the axis (this being judged by the eye alone) will necessarily introduce marked errors which may be estimated by the comparison of several sections. With its many obvious faults, however, it is interesting to measure such a figure, and see what it will give: since such a drawing illustrates *all there is to be seen* at this plant-apex. The growing system has been checked at a given stage; at any other moment of growth it would present just the same appearance, some primordia growing older as others come on, around the circumference of the growing-point.

No further evidence of the production of a phyllotaxis-system is available: the method adopted is simple but imperfect: the point is to see if it is sufficient for the purpose. It being quite clear that what is wanted is a complete understanding of the whole of the facts given by one apex; and this can be done better on a large drawing than by observing the image in the microscope.

The first thing to do is to measure up the figure, and collect all the data—the length and breadth of the members, the angle subtended by each, and the angular divergences between successive numbers. The last is rendered possible in the case of older primordia, in which the first production of protoxylem gives a central point to the member, with considerable accuracy. The youngest leaves (0, 1, 2, 3, 4) can give only approximate values.

The subjoined table includes the results checked for this particular apex (the figure being a reduced copy of the original, and not necessarily accurate), and the following features may be noted:—

Number of leaf.	I Radial depth in mm.	II Tangential breadth in mm.	III Ratio of preceding.	IV Angle subtended at centre.	V Angular divergence. First estimate.	VI Angular divergence. Second estimate.
0	—	—	1 :	—	—	—
1	12 mm.	15 mm.	1.25	39°	137.5°	136°
2	14	17	1.21	38	135	137.5
3	16.5	25	1.51	59	137.5	134
4	15	25	1.66	56	142	143.8
5	17	30	1.76	61	127	129
6	19	35	1.84	67	142	140.3
7	19.5	39	2.00	66	137.8	139.5
8	23.5	46	1.91	76	132.7	132
9	28	53	1.82	79	145	143
10	24	55	2.29	76	131	133
11	32	72	2.25	92	140	138.8
12	31	75	2.42	86	138.3	137.4
13	35	86	2.46	90	132	132
14	44	100	2.27	96	143	141.3
15	39	102	2.62	90	136	137.3
16	45	120	2.66	95	136.9	136
17	46	125	2.72	90	137.3	136.8
18	—	—	—	—	—	—

Apex of *Sempervivum calcaratum* (3+5), Fig. XII.

(1) The pattern is a well-marked (3+5) construction, since 9, 14, 17, 12, or 4, 7, 9, 12, for example, give a rhomb of contact: the longer '3' curves are clean-edged, while the '5' curves are very slightly 'stepped' after about two cycles. On looking up the table for such a system,¹ the angle subtended by a quasi-circle primordium should be 61° 44'. That subtended by a full quasi-square rhomb, 85°. The divergence angle is 137° 38' 50".² The ratio of the length to the breadth of the quasi-circle is 1 : 1.004.

At first sight the standard of reference does not appear to give any very great assistance.

(2) Circular tangential paths drawn through the central bundles of the older leaves indicate that these leaf-primordia are obliquely orientated: this being associated with the assumption of a more rhomboidal form as they

¹ Rel. Phyll. Mech. Laws, pp. 338, 340.

² loc. cit., p. 340.

are pressed into close contact relations. That is to say, 'quasi-circle' primordia tend by contact-pressures to become 'quasi-squares'.

(3) The youngest primordia are rounded, but distinctly less radially extended than the theoretical quasi-circles, No. 1 giving a ratio of 1.25:1, instead of the theoretical 1.004:1. That is to say, the youngest visible primordia are already possibly radially reduced in growth; and such reduction extends progressively until at No. 17 the ratio of breadth to radial depth is 2.72:1. This implies that there is a progressive radial retardation in the rate of growth throughout the entire system, and it has already set in when the primordia first appear as visible protuberances.

(4) As the angle subtended at the centre (Column IV) also steadily increases, it would seem that there is an increase in the rate of tangential extension; but this is probably largely a subjective effect; since the primordia are gradually pressed into the form of contact quasi-squares, the angle subtended by which would be 85° . Other causes also come into operation in dealing with the tangential dimensions of older leaves, which may be cut at a slightly higher level than their successors: the extension beyond 85° , as a matter of fact, is not very considerable in this case.

(5) In the first column the succession of radial dimensions does not increase in exact progression; and the same applies to Col. II for the tangential extension: there are again inequalities in the ratio of these measurements as expressed in Col. III. Such inequalities are clearly the expression of the error of the section, especially from the standpoint of obliquity in the exact transverse plane. This is again emphasized in Col. IV. The angles subtended by Nos. 3 and 11, for example, are much too large; so to a less extent are those of 14 and 16. Assuming that these young leaf-primordia are broader below, it would appear that the section dips a little on the top left-hand corner.

(6) Since the angle normally subtended by a primordium filling its place in such a contact-system should be 61.44° , it would appear that the members indicated as 1, 2, 3, &c., are smaller than they should be if the mechanism of the pattern were determined solely by conditions of bulk-ratio. This again eliminates the standpoint that the mere size of the primordium as it first appears has any necessary connexion with the construction to be worked out. In fact, the angles subtended by the youngest primordia would even suggest the initial points of a (5+8) system, the primordia of which normally subtend $30^\circ 10'$. On the other hand, the system can be only taken as it stands; and it is called a (3+5) because the majority of the members are in this contact-relationship. It is sufficiently obvious that the number of patterns seen varies according to rates of growth. In this particular case, for example, the older leaves of the bud may present a definite (5+8) arrangement, quite distinct from the apical construction.¹

(7) Special interest attaches to the *divergence-angles* measured from the protoxylem-points for 13 leaves, and approximated from 1-4. Conspicuous errors are at once indicated, rendering any very exact use of the method very doubtful: for example, Col. V gives a range between 127° and 145° ; Col. VI (with a difference of 1 mm. on the drawing, in estimating the centre of the system) a range of 129° - 143.8° . The true centre probably lies nearer the latter than the former. As 5, 8, 10, 13 are conspicuously low, and 6, 9, 14 conspicuously high, the position of these members clearly indicates that they are affected by the inequality of the section. On the other hand, errors of centring and the obliquity of the section will be eliminated on taking averages.

¹ loc. cit., cf. p. 244.

Thus the average of the entire set of 17 leaves (Col. V, VI) gave 137.11° and 137.04° respectively, as opposed to a theoretical angle of 137.65° .

But since any successive 5 members in such a system should make mathematically similar contact-cycles around the stem, it is interesting to take averages of members successively 5 at a time. On doing this it will be found that these averages range from 135.8° to 137.86° for the first column, and between 136.06° and 137.76° for the second. Or, omitting the first members, for which the central points were only approximated, the average of a cycle of 5 is always remarkably well within one degree of the ideal angle.

There is thus sufficient evidence in this apex of a remarkable approximation to a divergence-angle of about 137° , in a system which is at the same time undergoing radial retardation, and subject to mutual contact-pressures which tend to produce a rhomboidal contour in the members.

(8) Even more remarkable is the fact that the divergence-angle remains equally constant throughout the series, so far as can be measured. As opposed to Schwendenerian theories of displacement, there is not the slightest indication of any 'lateral displacement'. No member has slipped out of its relative position owing to the effect of hypothetical contact-pressures. The error of the Dachstuhl-hypothesis is at once demonstrated by systematic measurement.

(9) It is also evident that in an Archimedean system, as that of Schimper and Braun, which would be attained when the adult members show equal radial depth, the divergence-angle must become $\frac{3}{8}$ of $360^\circ = 135^\circ$. But so far in this system, which covers still growing members, there is no sign that such a secondary divergence-angle is being produced. While again there is sufficient evidence that the members here are not yet attaining the equal depth of the adult condition (Column I), and that such mathematical relations do not obtain.

(10) The fact remains that, allowing for the errors of the section, a system of measurements may be sufficiently accurate to reasonably demonstrate that the angle of 137° is very fairly and uniformly approximated by the plant; and that the angle is practically a constant, however the system may vary its growth-phenomena in other respects.

The same method may be applied to other plant-apices with closely similar results. One other example may be taken, of an apex which differs in many respects from that of *Sempervivum*. Tips of *Cobaea scandens* are of interest as affording examples of leaf-systems in which practically no contacts obtain between the young members; and yet each young leaf stands well away from its neighbours, with its own well-marked angular divergence. Section shows that these primordia are rapidly differentiated and segmented into compound laminae, but still remain well-spaced apart. There are no contact-pressures, no squeezing into quasi-square rhombs, and hence no slipping of the angles; while the exact bilateral symmetry of each leaf with regard to a radius passing through the central point of the vascular system is a most striking feature of the construction. (Fig. XIV.)

A similar camera lucida drawing shows leaves in a $(3+5)$ system numbered 1-14, and the divergence-angles are measured as before. The youngest protuberances are still indefinite, and leaves with the protoxylem indicated range from 7 onwards. Omitting 14, which has been already displaced in making the preparation, as shown by its asymmetry with regard to the radial plane, the average of cycles, taken 5 at a time, is 137.36° , 137.8° , and 137.2° respectively. The general accuracy of the method is thus in close general agreement with that found in the case of *Sempervivum*, though over a more restricted field, and again indicates an undoubted approximation to the Fibonacci angle of $137\frac{1}{2}^\circ$, or to the theoretical angle of the construction-system $(3+5) = 137.65^\circ$.

Cobaea scandens, Fig. XIV.

No. of leaf.	Angular divergence.	
1-2	151°	Average of cycle of 5.
2-3	133	
3-4	137	
4-5	135.3	
5-6	138.5	
6-7	143	
7-8	135.2	
8-9	134	
9-10	133	
10-11	133	
11-12	133	
12-13	—	
13-14	—	

There is no need at this stage to multiply further examples. It is sufficient to state that similar results are the general property of plant-apices with constructions expressed by such low numerals as (2+3) and (3+5).

But it may now be taken as demonstrated that:—

(1) *There is a very definite approximation in such systems to an angle of 137°, or 137½°; which for convenience may be labelled the 'Fibonacci Angle' of plant-constructions.* While the *Ideal Angle* of Weisner is 137° 30' 28.936", and the angle given by the Equipotential Theory for a (3+5) construction is 137° 38' 50".

(2) On the other hand, *there is no evidence available in the plants at present of any closer approximation to these data, which remain those of a standard of reference.* The plant gives an angle sufficiently accurate to suggest that both these latter conceptions may be correct; but there is no need either to postulate or to imagine absolute agreement or precision in the plant-construction. It may be so, but there is no means of practically demonstrating the fact. The data given by the plant and the mathematical data of the calculated standards require to be kept perfectly separate.

No greater accuracy of measurement can be obtained in a whorled construction, which is regarded as presenting exact circular symmetry. The smallest consideration shows that the circles of a plant-apex are never mathematically accurate, and the spacing of the members of the whorls is only approximated, however beautiful the effect may be to the unaided eye. Here again mathematical calculations of the angles, &c., are only useful as a standard reference. Once mathematical considerations are introduced into such a subject, a curious obsession, that since the mathematical data are so exact, the plant substance is necessarily obliged to work in an equally precise manner, becomes a general fact of belief extremely difficult to eradicate.

(3) Still, though there is no evidence that more accurate angles are attained in the plant-construction, *this general approximation to the angle 137½° is the great outstanding fact of Fibonacci phyllotaxis.* This angle is obtained from the plant by observation only: other phenomena associated with it are subsidiary, and confirm the idea that the constancy of the angle, within quite a small range, is the central feature of the entire subject, and is the fact which has to be accounted for.

The problem remains, therefore,—How is this angle adjusted or obtained at the plant-apex? Where does it come from phylogenetically? and above all—By what mechanism can it be maintained in a growing shoot-system?

VI

THE MECHANISM OF PHYLLOTAXIS

AN angle of approximately $137\frac{1}{2}^{\circ}$ has been termed the Fibonacci angle, in contradistinction to the 'Ideal Angle' of the Schimper-Braun notation; the latter a purely mathematical abstraction, while the former is an established *fact of observation* taken directly from plant-constructions. The value of this angle is so peculiar, that no reasonable person can further refuse to believe that it actually represents an approximation in the plant-organization to the theoretical Ideal Angle ($137^{\circ} 30' 28.936''$) which would afford maximum illumination to the leafy system if vertically displayed; and that this is no mere coincidence, but a phenomenon of such wide occurrence that it must undoubtedly afford some clue to the remarkable problems of shoot-construction. But such phenomena, as expressed in the constancy of the angle, even if no more accurate than the angle accepted (of about $137\frac{1}{2}^{\circ}$), require a mechanism for their production; and it is naturally in this mechanism that the whole of the physiological interest of the subject is centred. One gets little further, for example, by supposing that an originally irregular development of aimless 'enations' settles down to a rhythmic process;¹ because, in spite of the 'Strobilus-Theory', there is no sign of such a proceeding in land-vegetation. An indefinite protuberance (provided for botanically as an 'emergence') has not necessarily the very striking and peculiar attributes associated with a 'leaf'-appendage;² an adventitious shoot is an organization of a quite different category; while it may be noted that the mechanism for producing one 'enation', as also even one pseudopodium, must be quite distinct from the mechanism which involves a serial repetition of the act. It is in fact this *rhythm* which demands the essential mechanism; and the evolution of, or the necessity for, such rhythm is the fundamental feature of the problem. The question remains, therefore, as to where such a mechanism can be seen or traced.

In regard to this, at the outset, one point may be granted as firmly established:—the mechanism has no relation whatever to the more obvious cell-framework of the plant-apex. It is only necessary to examine a longitudinal section of such a growing-point to see that there is *nothing visible* beyond the dividing cell-meristems. New primordia arise, as seen in section, as waves of lowest elevation, often involving a considerable number of cells from the first; there is no sharp demarcation of such undulations, nor can it be said where to a single cell each exactly begins or ends. The protoplasm of the apex may be preferably regarded as a mass of fluid colloidal plasma, in which the secondary production of denser colloidal cellulose films may have but little effect on the physical

¹ Bower (1908), 'Origin of Land-Flora,' p. 141.

² R.P.M.L., p. 190: a remarkable case being presented by the form and arrangement in alternating whorls of the emergences on a syncarpous ovary among Palms of the section *Lepidocaryinae*: *Rahia Ruffia* (6 + 6).

condition of the living and fluid mass as a whole. The remarkable example of some Vascular Cryptogams, in which the cell-units may be produced in one rhythmic and spiral sequence, apparently dominated by a single apical cell, while the leaf-members arise either in a wholly different spiral sequence (*Aspidium*), or even in symmetrical circles (whorls of *Equisetum*)—in which the apical cell still independently cuts off segments in spiral sequence of three rows, again apparently controlled by the orientation of the rotating nuclear spindle of the apical cell itself—shows at once that the mechanism underlying leaf-production in higher Land-Flora must be something quite distinct from cytological details. The mechanism of Fibonacci phyllotaxis being thus:—

- (1) Sufficiently accurate to attract attention as being restricted to a divergence-angle of about 137° .
- (2) Completely independent of cell-segmentation.
- (3) Due to some wholly invisible cause beyond the reach of microscopic observation.

Some suggestion has to be made as to what it may be; even if nothing more be gained than a working-hypothesis.

If the mechanism is then invisible, there is really no escape from the conclusion that it must be in some way molecular, in the sense that crystallization, for example, may be termed molecular. This is the next natural step to consider: when molecular properties fail, it may be time to pass on to something even more abstruse. But at this point the botanist who is interested in things seen, or which can be treated experimentally, has to stop. Molecular mechanisms still wait on the physicist. The botanist has to be content with a working-hypothesis which will include all the facts of observation. The first point at issue, therefore, is how to account for this constant approximation to a divergence-angle of about 137° . Once the standpoint of cell-control is eliminated, the possibilities of explanation open to the botanist are obviously restricted. The first most natural view to discuss is that of the traditional 'Genetic Spiral'. Is it conceivable that a plant-apex of undifferentiated meristem has the power of measuring off angles of about $137\frac{1}{2}^\circ$ at stated intervals with a considerable degree of accuracy and constancy, and that the subsequent pattern is the result of two such associated factors—one of exact angular measurement, and the other involving a time sequence? An angle of $137\frac{1}{2}^\circ$ is not easy to obtain by human geometrical methods, and there is no sign how it may be measured in the plant. It is of course possible that such might occur; but if this be the case the problem remains hopeless of further solution, since there is no trace of any mechanism which will produce the given effect. If the teleological generalizations of Wiesner held to such an extent that the Fibonacci angle was compulsory for all shoots devoted to photosynthesis, it might be conceivable that such an angle, having been attained at some distant period, had become fixed by natural selection, to remain constant or ingrained in the plant-organization, and so heritable. But this is not the case: the angle $137\frac{1}{2}^\circ$ is after all but one of many. Shoots of the same plants which otherwise build accurate Fibonacci systems will give other patterns based on equally constant divergence-angles;¹ the angle may be readily changed, yet remain constant until changed again. That is to say, we might imagine one hypothetical simple mechanism that would always give the same angle of $137\frac{1}{2}^\circ$ in all plants; but we cannot so readily imagine a simple mechanism that would equally well repeat almost any angle with equal regularity.

¹ R.P.M.L., pp. 101, 104; *Araucaria, Podocarpus*.

In fact a merely cursory examination of the general problem of phyllotaxis among subaerial vegetation is sufficient to show that the divergence-angle can have no primary causal relation, but is now itself the consequence of other factors, following as a mathematical property of the numerals involved in the spiral pattern, as expressed by the number of parastichies,¹ whatever may have been its original significance.

Again the data presented by the apex of *Sempervivum*,² for example, about which there can be no doubt whatever, are:—the system is a growing and expanding one, producing leaf-members (1) at a fairly constant divergence-angle of $137\frac{1}{2}^\circ$, and (2) presenting a set of curves making a pattern in which 3 paths cross 5, i. e. (3 + 5). If the former phenomena be dismissed as too vague for practical consideration, one can still fall back on the latter. There is no further choice. Is such an angle of $137\frac{1}{2}^\circ$ obtainable from any possible construction involving the numbers 3 and 5? Yes, it is a problem of uniform mathematical growth, the solution of which states that orthogonally intersecting logarithmic spirals equally spaced in this complementary ratio will give successive intersections at $137^\circ 38' 50''$;³ and this is the simplest solution possible. We are therefore bound to take it as the next standpoint for consideration: if it fails, further discussion will be necessary.

The Equipotential Theory simply accepts this mathematical generalization as the basis for further elaboration; and suggests that nothing more is required. The problem is solved once for all. Instead of a wholly miraculous mechanism repeatedly measuring off angles of $137\frac{1}{2}^\circ$, the proposition reduces to a question of 2 relatively simple numerals involved in a special but visible geometrical construction.

Even so the question of mechanism remains sufficiently wonderful: but a simple analogy may render the suggestion a little clearer. Few features are more remarkable, yet always accepted without question, as a commonplace of elementary botany, than the initiation of the protoxylem points in a typical Dicotyledonous root. Nor is the mystery underlying this problem rendered any clearer by suggesting that the few protoxylems of such a root are the specialized relics of a polyarch xylem, or of a uniform exarch xylem-cylinder. Centres are isolated in small and variable number at approximately equal distances, in a special region of the stele, and these control not only the subsequent anatomical differentiation of the root, but its system of subsequent ramification. Analysis of this comparatively simple phenomenon shows that 4 factors are involved, which must be actually represented in the apical meristem:—

(1) *A power of numerical choice.* The number is fairly constant, though within certain well-defined limits; one numeral being selected by each apex: e. g. 2, 3, 4, 5, or 6 in many common plants (*Pinus*, *Quercus*). We do not know how the apex has the power to count; or how the number is regulated; but the numeral for each root is a fact of simple observation.

(2) *A factor for equal spacing.* Whatever numeral may be selected, the individual points are approximately equally spaced around a circular path: i. e. 2 at 180° , 3 at 120° , 4 at 90° , &c. We do not know to what extent these angles are accurate at the moment of initiation, or only roughly approximated. As there can be little advantage in accurate spacing, it is usually considered teleologically that the arrangement is only approximate. But both the arrangement and the spacing are again facts of observation.

¹ R.P.M.L., pp. 218, 234.

² loc. cit., *Sempervivum*, pp. 16, 244.

³ loc. cit., p. 340.

(3) *The pattern expressed by such a series of exarch protoxylems spaced round the periphery of the stele, is really, from a geometrical standpoint, an orthogonal system in which radii intersect a circular path at right angles: i.e. the impulses of xylem-differentiation proceed centripetally at right angles to the surface of the stele.*

(4) *This remarkable delimitation of new centres of differentiation is restricted to a definite region of the root, and so accurately localized that it is possible to define the pericycle in exact histological units with regard to them.*

Now comparison of the phenomena to be explained at the apex of a stem in the initiation of a phyllotaxis-construction shows that the analogy is sufficiently close to be very striking. The same 4 factors are involved in both cases: the only difference being that the case of the shoot-apex is somewhat more elaborate geometrically, but not in any other respect. Thus:—

- (1) The power of numerical choice involves 2 usually quite simple numbers.
- (2) Equal spacing is provided by the geometry of log-spiral systems which may be continued with the growth of the plant 'to infinity'.
- (3) The resultant pattern involves orthogonally intersecting generalised curves, of which the radius and circle are only limiting cases.
- (4) The production of new centres is restricted to surface-layers of the shoot (epidermis and exo-cortex), less defined than in the case of the root; while these centres, once initiated, are subsequently utilized to continue the space-form of secondary ramifications.

It is difficult to avoid the general conclusion that the growing root-apex has a power of numerical choice, within certain limits, and not necessarily constant; as also a faculty for equal-spacing in order to give a balanced result. How is it done? We can so far form no real opinion; the mechanism is beyond the range of visibility, and hence we simply accept it as a fact of observation. Yet it is evident that a fixed number of 'impulses', of some description, must radiate from the growing-point along certain equally-spaced lines of distribution, which affect a region of certain tissue-units only. That is to say, the path of the impulse is *numbered, spaced, and limited.*

Very closely identical phenomena must be similarly characteristic of the shoot-apex:—*impulses of definite number, equally-spaced and restricted to narrow paths, apparently radiate from the growth-centre, in two opposite directions, and with exactly equally balanced distribution, as in the typical case selected, 3 in one direction and 5 in the other. The points at which these impulses intersect give the initial points for the commencement of a lateral appendage. The impulses are invisible, but the effect at the point of intersection is seen in the initiation of a new growth-centre which is restricted to the surface-layers of the apex. This new centre, again, differs wholly from the parent growth-centre in its segregated factors. It initiates an entirely new set of growth-phenomena; some the expression of the mechanism of the correlation of the new primordium with its parent centre (factors of the quasi-circle), others the inherited product of the past natural selection which has given the leaf-member its special characters.*

Geometrical considerations, comparable with those which enable us to say that an equal spacing of protoxylem in a tetrarch root would place them 90° apart, again enable us to deduce the geometrical consequences which follow from a mathematically perfect system of equal distribution. But just as an error of 5-10° in the case of a root-*protoxylem* would not excite any special remark, so there is no reason to postulate the exact mathematical spacing of these impulse paths, since they cannot be checked

by observation; the use of the mathematical discussion is again solely that of affording a standard of reference. The exact application of the Theory of Equipotential should now be clear. With regard to the power of choice, as expressed by 2 numerals in the shoot-apex, there is nothing to be said. It is even more vague than that of the single choice made by a root-apex; in that it may be at any time changed by the addition or loss of paths giving the great variation possible in changing phyllotaxis-systems. Yet we know by observation the possible and probable range of such choice, and that it is commonly restricted to the lowest ratios.¹ Nor do we know what is meant by 'impulses'; whether classed as 'paths of distribution', 'lines of force', 'paths of nervous tension', or any other vague expression with which ignorance may be clothed. But the mechanism of equal spacing can be studied mathematically, and it is given in perfect form by the equipotential construction in terms of orthogonally intersecting spirals. It is thus open to argument that it is from a certain demand for equal spacing that the orthogonal construction follows; and that the recognition of a geometrical construction comparable with spiral vortex-construction, or with propositions of electric potential, is here paralleled by the plant from a purely geometrical standpoint, rather than as indicative of any fundamental agreement in an expression of distribution of either kinetic or static energy. This in fact is the first objection of the physicist.

Propositions of equal spacing can, however, be as readily worked out for any angle of intersection so long as the angle remains constant.²

The critical point lies in the fact that the angle in actual growing plant-constructions is never maintained as a constant, and in the possibility that a system of orthogonal construction may be significant of some deeper fundamental property of protoplasm. The whole point of the preceding investigation has been centred in an attempt to prove the significance of this property, by assuming its existence and deducing the consequences.³ Added to this, the remarkable agreement of the fundamental recognized properties of a leaf with the mathematical properties of the quasi-circle, even when inscribed in the orthogonal mesh of an asymmetrical construction, has been put forward as a sufficient proof of the truth of the idea; since no other simple mathematical generalization can give such a result. On the other hand, it has been suggested that orthogonal construction merely implies the utilization of the simplest angle to keep adjusted, and that the geometry of the construction is perhaps the end of the mathematical possibilities. But even here, such a view cannot represent the whole truth; since in dealing with a living mass of protoplasm we still have to account for the possibility of the evolution of such a mechanism in the plant. From such a phylogenetic standpoint it is scarcely possible that such a geometrical system could have been originated, unless it had in some way utilized features of construction which were pre-existent, as some attribute of the molecular forces of growing protoplasm.

In the narrowest sense, then, the equipotential theory remains as a standard of reference for the rules of equal spacing: in a wider sense, still to be hoped for, as put forward when the proposition was first

¹ R.P.M.L., cf. p. 342.

² Misled by an enthusiasm for drawing pretty but meaningless figures, Van Iterson has in this way attempted to improve on the log-spiral constructions originally put forward as sufficiently satisfactory; regardless of the simple fact of observation that in no growing system in a plant-shoot do the parastichy curves continue to intersect at any constant angle! G. van Iterson, jun., 'Blattstellungen,' 1907.

³ R.P.M.L., p. 230.

enunciated, it may give a clue to the more obscure workings of protoplasmic growth, and prove in fact the first efficient step in the progress of an effective plant-morphology. While, however, these remoter possibilities remain very much in the air, it is so far important to note that all mathematical and geometrical considerations are to be regarded solely as a standard of reference for phenomena which may be exact enough for the biological purposes of the plant, but are not necessarily absolute. Still that is no reason why geometrical constructions should not be followed up in order to widen the scope of the inquiry.

Above all, it is essential to attempt the investigation of the actual phylogenetic origin of such a remarkable series of phenomena. Interpretations of the growth-factors of subaerial vegetation founded on hypotheses of subaerial evolution from Cryptogams of fresh-water ponds have proved singularly unfortunate in other departments of Botany. The possibility remains that the phyllotaxis-mechanism of the shoot-apex of a higher plant of the land is after all but the highly modified or elaborated version of some much older if more obscure ancestral organization, adapted to present conditions of environment it was never designed to meet. Once it is understood that biologically every factor of organization must be inevitably an adaptation, possibly the end-term of some preceding sequence of successful adaptation in the long-continued progression of plant-life, mere teleological interpretations of subaerial forms become meaningless, and the attempt should be made, if possible, to trace such phenomena of plant-organization to first causes.

VII

PHYLLOTAXIS-PHENOMENA IN CRYPTOGAMS AND THALLOPHYTA

RHYTHMIC expressions of leaf-arrangement are by no means confined to higher plants or Phanerogams, the Seed-Plants of more dominant Land-Flora. Very elegant applications of the general principles are to be seen among Pteridophyta, in which leaf-members are similarly arranged on axes of a sporophyte-generation; and it is sufficiently obvious that while higher types of vegetation have passed through such a Pteridophyte phase, the mechanism of their leaf-arrangement has been similarly inherited from the more distant epoch of the transmigration to land, and the attainment of the soil-habit by the first land-plants. On the other hand, arrangements involving rhythmic spiral succession are equally characteristic of higher Bryophyta of the Moss-series (Bryineae); though in this case the phenomena are to be traced in the gametophytic (sexual) generation, in which, owing to the inefficiency of the absorptive mechanism, the full anatomical details of a transpiring leaf-lamina are never attained; yet it is difficult to withhold from such seriate appendages of the Moss-axis the morphological value of 'leaf'-members in these vestigial relics of more archaic transmigrant types. The case is again complicated by the fact that very admirable spiral arrangements, in which Fibonacci symmetry may be distinctly traced, obtain in the case of many of the more massive Brown Seaweeds (Phaeophyceae-Fucoideae), in the orientation of the more or less frondose or leaf-like lateral ramuli; leaving little doubt that the phyllotaxis-mechanism is, in fact, a still older function of the axis of marine types of vegetation, and

that the presentation of such phenomena, even in a more elaborated and special form, can be but the continuation and amplification of factors of marine phytobenthon; and that it is to the sea that one must look for the origin and primary intention of this remarkable relation. Even behind the horizon of the more massive parenchymatous marine alga, it is possible to trace, even back in the plankton-phase, distinct expressions of spiral organization associated with Fibonacci ratios; not, it is true, among autotrophic phytoplankton, but all the more remarkably in that similar appearances may be exhibited in holozoic and animal forms of life among the great group of the Foraminifera.

I. Pteridophyta. The tendency of the general run of Filicineae to produce their leaves in spiral sequence, as also predominantly in terms of ratios of the Fibonacci series, may be accepted without discussion as a simple fact of observation. The example of the apex of *Aspidium Filix-Mas*,¹ has been adduced as affording the most perfect expression of the complete independence of the individual primordia of such a sequence from contact-pressures in early stages, as also for their derivation from the tissues of the apex without any regard whatever for the 3-sided apical cell, or the spiral of its successive segments. Variations on the theme may, however, supervene, as:—

(1) Irregularities in construction, as expressed by the addition (or often loss) of construction-curves in the system, exactly in the manner of irregularities in the axes of Cactaceae and Cycads, and similarly the expression of a deteriorated mechanism. In large tree-ferns the curves may be 'anything'; and in special cases it is possible to trace, by the equalization of the curves in either direction, the attainment of symmetry, general or partial only, giving a precise whorled effect (*Alsophila*).²

(2) In cases of advanced dorsiventral organization, the construction may reduce to $(1 + 1)$, with the plane of bilaterality correlated with dorsiventral symmetry to give two rows, right and left of the axis, familiar in the type of *Pteris*, clearly the highest expression of advanced specialization, and by no means 'primitive'.

(3) In the highly specialized dorsiventral shoots of Hydropterideae, whorled symmetry may be associated with the dorsiventral habit, involving a special condition of orientation and leaf-presentation, as in the essentially decussate $(2 + 2)$ system of *Azolla*, and the remarkable $(3 + 3)$ construction of *Salvinia* with marked heterophylly in the whorls.³

In spite of advancing specialization, or general decadence, the type of the Filicineae may be said to be primarily based on Fibonacci symmetry. More marked is the case of *Equisetum*, in which a similar 3-sided apical cell-mechanism is associated with whorled symmetry in leaf-production, giving 3 members to a whorl in the limiting case, but readily rising to over 30. Variations in the case of *E. Telmateia*, the finest available form, have been recorded (loc. cit., p. 147), while the occasional production of spirally constructed shoot-systems, over the whole or a portion of their length, as a 'monstrosity', has been shown to follow the mechanism of the simplest variant from symmetry, as the case of the $(m : m + 1)$ ratio. It may be accepted that the symmetrical constructions of *Equisetum* are wholly secondary, and are associated with extreme xerophytic habit, giving a sequence of alternating whorls when the construction remains constant for

¹ 'Relation of Phyllotaxis to Mechanical Laws', p. 29, Fig. 35.

² Ornamental vases being cut from a stem thus presenting a symmetrical pattern in the sclerosed plates associated with the stelar skeleton.

³ R.P.M.L., loc. cit., p. 280.

any definite number of internodes. That this special case of phyllotaxis-mechanism is of extreme antiquity follows from the constancy of the same whorled construction in all fossil records of allied Equisetinae. The secondary regression to a spiral freak is exactly paralleled among Angiosperms in the cases of *Hippuris* and *Casuarina*.

Among Lycopodiaceae spiral construction is again dominant in the more elementary types of shoot-construction, cf. *Lycopodium* and *Isotetes*; though decussate symmetry also widely obtains, and may be associated with an advanced phase of secondary dorsiventrality, as in the general type of *Selaginella*, as based on the earlier spiral construction of *S. spinulosa*. Illustrations of the extreme range of numerical schemes in the case of the decadent *Lycopodium Selago* have been given (R.P.M.L., loc. cit., Figs. 78, 79, 80); the association of (5 : 5), (4 : 4), (3 : 3), and (2 : 2), emphasizing the readiness with which such symmetrical variations follow from constructions as (5 : 6), (4 : 5), of the ($m : m + 1$) order: the last being recognizable variants of Fibonacci ratios, as seen in the case of other xerophytic types, cf. *Palaecarpus* (loc. cit., Fig. 104) and *Sedum* (loc. cit., Fig. 104).

Of special interest again are examples of spiral construction cut in calcite sections of calcified coal-balls of the Carboniferous Epoch. Though really accurate transverse sections of the actual apex may be rare, and the latter will be decomposed, sufficient evidence is forthcoming to show that Fibonacci relations prevailed at this early period, quite as well as to-day; and the construction may be as readily interpreted.

Thus Stopes ('Ancient Plants,' 1910, p. 136) figures a *Lepidodendron* apex with curve-construction very clearly expressed of the 4 : 7 : 11 form; the actual apex is naturally somewhat damaged, but the type presented is that of a normal secondary 'anomalous' ratio.

Scott ('Studies in Fossil Botany,' i, 1908, p. 137) gives a section of the young stems of *Lepidodendron Harcourtii*, with the vascular trace-bundles of the outer cortex retaining their spiral orientation in a very definite system which may be expressed as (9 : 14), again only a minor variation on (8 : 13), and again clearly referable to such deteriorated mechanism as may be found in a tree-fern or Cycad-axis.

An interesting example from an unnamed *Lepidostrobus* axis (cut by Leomas, Bot. Mus., Oxford, No. 43) illustrates very clearly the curve-system, as expressed by the remains of the trace-bundles of the macerated stem, of the form (8 : 13); the Fibonacci-ratio being definitely present as an unmistakable example of its occurrence; and the phyllotaxis of such a cone may be so described in lack of further evidence of the apical construction (Fig. XV).

On the other hand, it is interesting to note that the distribution of the trace-bundles of an axis, although affording a curve-pattern in terms of the ratio-series employed, does not necessarily give the actual construction at the growing-point itself; since secondary growth-phenomena may space the members differently in older parts of the same shoot as they become adult (cf. R.P.M.L., loc. cit., p. 325). Thus a slide of *Lepidodendron* (kindly lent by Prof. Oliver, Univ. Coll. Collection, *Lepidostrobus pilosus*) shows quite distinctly the trace-bundles of the axis, in spite of partial maceration, in a system which would be described as (7 : 11); but the section nearest the actual growing-point shows the young leaf-primordia very distinctly in a contact-series of (3 : 4), though opening out at the periphery of the section to (4 : 7), and ultimately (7 : 11), with diminishing rate of growth in the leaf-members.

Probably the actual apex of all *Lepidodendrons* was expressed in comparatively low numbers, just as in the case of modern Gymnosperms (cf. *Arceuthobium excelsa*), and there is no need to wander into complexities of hypothetical high divergence-fractions, deduced from the consideration of the leaf-base scales of older axes. (Scott, loc. cit., p. 128.)

Thus allowing a margin for (1) secondary assumption of symmetry

(2) secondary attainment of dorsiventrality, (3) deterioration of the mechanism, either in non-photosynthetic strobilus-construction, or in deteriorated and reduced axes,—all phenomena largely associated with extreme biological adaptations for special and usually xerophytic environment, or the elaboration of reproductive shoots of limited growth,—the Pteridophyta appear to be as constant to the general mechanism of leaf-production and the ratios of Fibonacci orientation as are the corresponding ecological and floristic developments of higher Angiosperm vegetation; and the phenomena of primary Fibonacci orientation are to be traced unchanged at least as far back as the beginnings of Vascular Plants.

II. Bryophyta. The case of the Bryophyta runs on distinctly different lines, in that the leaves are produced by the apical-cell mechanism of a gametophyte-axis, now dominant and controlling the segmentation of the apex both into cells and members. The mechanism is still essentially that of the same 3-sided apical cell as found in Filicineae and Equisetineae, and is similarly the expression of the rotation of the nuclear spindle in successive mitoses, as affording the minimum condition of three-dimensional (centric) organization. Such a mechanism, if perfect, would be expected to give leaf-members in 3 vertical orthostichies, arranged with a divergence of 120° . This may be fairly approximated in a few examples, as in the case of the submerged moss *Fontinalis*, growing in weak light with an elongated axis, with the leaves on the adult shoots running in 3 only slightly curved 'spires'. In the more normal type of the Eubryales the leafy Moss-shoot presents characteristic Fibonacci symmetry, and formulae for leaf-arrangement have been commonly tabulated in the fractions of the Schimper-Braun notation, and even in anomalous series, though it must be said on very slender evidence. Thus Müller (1894)¹ gives *Fontinalis* as ' $\frac{1}{3}$ divergence', and the adult effects of others produced by 'torsion'; as commonly ' $\frac{2}{5}$ ' (*Sphagnum*), $\frac{3}{8}$ (*Funaria*, *Bryum*, *Mnium*), $\frac{5}{13}$, $\frac{8}{21}$, $\frac{13}{34}$, as also fractions of other series as $\frac{7}{17}$, $\frac{4}{11}$, but never whorls. *Polytrichum commune* is scheduled $\frac{5}{13}$, *P. piluliferum* $\frac{8}{21}$, and *P. formosum* $\frac{13}{34}$.

The effect in the adult axis may be more readily understood by cutting a transverse section of the stem of *P. commune*, and noting the orientation of the trace-bundles of the leaves, in the manner described for *Lepidostrobus*. The figure (Fig. XVI) illustrates the fact that the trace-bundles pass vertically down the axis in 3 curve-systems corresponding to the three lines of successive segments; but an apparent 'compensation' enables them to be spaced out, and the divergence-angles may be very approximately measured by taking the radial median line of the leaf-trace area. In this case about a dozen members may be fairly accounted for, affording 10 successive divergence-angles of 135 , 140 , 131 , 143 , 134 , 130.5 , 145.5 , 129 , 152.5 , 127.5 ; the average being 136.8° , with an individual range to 129° and 152.5° ; or taking the outermost better-expressed areas three at a time to avoid errors of centring, 135.3° and 135° : that is to say, a very suggestive Schimper-Braun angle, as expressed by the fraction $\frac{2}{5}$ of 360° , but equally to be regarded as the approximate derivative of a Fibonacci construction, in which a system in Archimedean notation is attained secondarily with the equalizing of the internodes of the adult axis. The mechanism of 'compensation' is introduced apparently in the actual apical cell itself, or its immediate derivatives, to the extent that the segment-walls are not parallel with that of the parent cell,² and this feature suggests directly that the Fibonacci condition of symmetry is the primary factor after all, and the mechanism of a 3-sided apical cell is adapted

¹ In Engler and Prantl (1894), p. 177.

² Müller, loc. cit., p. 178: Goebel, 'Organography,' ii, 131: Correns, 1899, in 'Untersuch. Schwendener', p. 385.

to it as far as it will go (Correns,¹ loc. cit., p. 390). The fact that bilaterality in the axis may be associated with a 2-sided apical cell in cases of extreme dorsiventrality (*Fissidens*), again suggests that the construction is a property of the apex of the shoot as a whole, and the details of the segmentation of the apical cell are really subsidiary. That is to say, instead of the 3-sided apical cell 'dominating' the orientation of the leaf-members, it is within the control of some more obscure mechanism of orientation inherent in the plant-apex. The serial production of leaf-segments by walls parallel to those of a tetrahedral cell does not accurately obtain, however much it has been the custom to regard such a mechanism as 'simple'. The fact that each cell-segment from the apical cell gives a leaf-member is associated with the close approximation of the resultant laminae while young in a terminal 'bud'-aggregation, affording the young primordia mutual protection in sub-aerial environment; and though the mechanism in certain limiting factors may run parallel with that of the stems of certain Pteridophyta, there is obviously no identity of organization, and the priority of Fibonacci organization in the scheme of apical growth is thus traced to the earliest trans-migrant land-flora.

III. **Algae.** Examples of spiral organization in ramulus-production among algae are restricted to the Phaeophyceae, in so far as these seaweeds alone present a 'parenchymatous' type of organization in their somata, at all comparable with the cellular anatomy of higher land-flora.

The thallus of *Chara*, based on a corticated filament, increasing by transverse segmentation of an apical cell, bears lateral ramuli developed at a later date from nodal units; while in the case of the Florideae the thallus is again always more or less based on a filamentous type of organization, often complex and obscure, but apparently never attaining the stage beyond that of dichotomy, polychotomy, or indefinite ramular formations. Types in which the lateral ramuli are more specialized, or acquire definite dorsiventral orientation, are restricted to axes of a single filament (corticated types), in the manner of *Chara*: e. g. in *Polysiphonia* the ramuli are associated with cortical units, and hence in building spirally, one member at a time, the construction takes on the appearance of a similar winding spiral ('staircase-effect'), giving balanced symmetry, but not a Fibonacci system (cf. *Chara* with a spiral system of one leader per node, and *Polysiphonia* with four cortical cells in each segment, giving a ' $\frac{1}{2}$ ' divergence).

Identical phases of somatic progression are associated with the apical-cell segmentation of Phaeosporaeae, as in *Sphaedaria*, *Desmarestia*, *Spyralia*, *Spirinatochmus*, giving bilateral or balanced (whorled) systems, but not Fibonacci constructions.

Among the more highly differentiated Fucaeeae (in the widest sense), apical segmentation in terms of a single '3-sided' apical cell is attained again as the limiting expression in building a centric shoot by one dominant cell with a 'rotating' nucleus: the massive ramuli are not clearly traced to any definite segment of such a cell, though spaced at fairly equal intervals. Such massive somatic outgrowths may acquire a certain individuality and specialization, as expressed in limited growth and special form-factors of their own, presenting anything from an elaborated bilateral frond-system to a simple scale-like growth; all stages may obtain between indefinite ramification and the localization of such laterals at the expense of the main

¹ Correns gives the angle of segmentation required to work out a Fibonacci sequence of $137^{\circ} 30'$ as $52^{\circ} 31' 4''$. The figure suggested is, it is true, by no means the general shape of the 3-sided cell of a Moss-apex, and the suggestion is so far only of academic interest. It may be noticed that such angles, being bounded by curved lines, are beyond investigation.

axis among *Cystoseireae* (in the widest sense) and the more specialized types of *Sargasseae* (including *Sargassum* and *Turbinaria*).

In these forms, so long as the organization of the shoot-system remains centric, Fibonacci relations are found to obtain; though the presence of the mechanism may be obscured by the fact that growth of the lateral ramuli is usually more open; i. e. not telescoped within the limit of a terminal bud which may be sectioned to show the accurate space-relations of the adjacent members. Further, in the case of larger frondose systems, the accidents of the moving medium prohibit any precise display of mutual relations or special orientation with regard to a fixed light-position. Hence the general plan of the shoot-construction is less noticeable; though in a few forms the apical construction may have attracted attention (cf. *Landsburgia*, *Cystoseira*).¹

In this way one is entitled to assume the existence, within the parenchymatous apex of the *Fucaceae*, of a structural organization apart from that of the cellular segmentation controlling the space-form of the lateral members of a centric shoot-system, and giving an optimum system of distribution, built one member at a time, and possibly of distinct benefit from the standpoint of the maximum illumination of the members of a centric shoot-system. On the other hand, the bilaterality of *Halidrys* does not give 'minimum superposition' since the frond-systems lie extended in a plane across that of incident light in a flowing medium, or held vertically erect by means of the pneumatocysts indifferently. Hence, though there are apparently two alternative constructions in the sea, one is not entitled to assume that they have been produced solely in response to problems of maximum and minimum illumination; there may be something else behind.

On the other hand one is justified in concluding that Fibonacci phyllotaxis was initiated in the sea, without any necessary connexion with the claims of insolation in land-vegetation. Its origin is to be looked for in the sea; although in transmigrant land-vegetation the system of construction may prove valuable under the new conditions, and so be retained as one of the most deeply ingrained construction-factors of the leafy shoot. It being so far clear from the organization of the *Fucaceae* that Fibonacci relations are older phylogenetically than the differentiation of the 'leaf' itself as a strict morphological entity (as defined in terms of subaerial vegetation).

In *Cystoseira ericoides*, a readily available and indigenous plant, the small subulate ramuli (3-5 mm.) are borne in more definite bud-aggregation (1-2 mm.) at the apices of growing shoots; though in the strongest of these the tendency of some of the ultimate ramuli to again bifurcate from the base, or to branch into two or three, commonly disturbs the effect of the pattern. Simpler results are obtained with smaller laterals, in which growth is less active and the ultimate ramuli remain prevalingly single; in general effect much resembling the smaller ramuli of such a plant as *Araucaria excelsa* on a smaller scale; the ramuli presenting no special trace of dorsiventrality and ending in a sharp point. In such a shoot a view of the terminal bud from above shows obvious Fibonacci symmetry; and though angular measurements cannot be given with any degree of accuracy, the general resemblance of the pattern to the Fibonacci systems of higher plants is very striking. In the bud figured (Fig. XVII) 10 members in different stages of growth may be distinguished, and number 6 falls in the gap between 1 and 3; there is thus no question of a $\frac{2}{3}$ divergence, though 9 is nearer superposition, as if referable to a $\frac{3}{8}$ system. The divergence-angles as measured in the figure are:— 132° , 127° , 142° , 154° , 127° , 130° for members 1-8, giving an average of 135.3° , again approximately a $\frac{3}{8}$ divergence of

¹ Oltmanns (1904), 'Algae', p. 505. Vaillant (1883), 'Flora and Fauna, Gulf of Naples': *Cystoseira*. Grubler (1896), *Bibliot. Bot.*, Heft 38, Taf. 7: *Landsburgia*.

Schimper, but well within the possibility of the Fibonacci angle 137.5° , where no accuracy can be guaranteed in measurement. It will be noted that— (1) Only a few members are available; the system breaks down at 10 because no more are in sight. (2) There is no accuracy in finding the centre. (3) The range of individual error is again large; e.g. 127° – 154° . In all these respects the phenomena closely approximate those of the *Polytrichum*-axis.

The critical value of this Fucoid apex centres in the fact that while the centric axis is dominated by a 3-sided apical cell, cutting off segments in three series, much as in the Moss, the phyllotaxis again, even if regarded as based on some derivation of cell-segments of the apical, presents undoubted 'compensation' in the organization of the apex as a whole; and the ramular primordia assume the Fibonacci orientation by a secondary growth-factor involving growth-distribution within the young shoot as a whole. Though there is no direct proof of segmental origin, the equal spacing of the 'leaves' may well suggest that there must be some correlation between the ramuli and the three rows of segments diverging from the apical cell; but whatever it may be is immaterial to the general organization. This may seem somewhat arbitrary so far as *Cystoseira ericoides* is concerned, but more conclusive evidence of such secondary 'compensation' is afforded by the associated example of *Halidrys*. Since in the latter, with an identical mode of apical segmentation (Oltmanns, 1904, p. 510) the lateral ramuli are 'compensated' by undoubted secondary growth-processes to give a condition of obvious bilaterality, and the laterals fall into two strict lateral orthostichies as a pinnate frondose type. That is to say, if *Halidrys* can convert a system derived from a segmenting 3-sided apical cell to bilaterality, so may *Cystoseira* change the same cell-organization to Fibonacci symmetry; since, assuming the 3-sided cell would give 3 orthostichies at 120° , the change from 120° to the 180° of bilaterality is much greater than the compensatory correction of 120° to $137\frac{1}{2}^\circ$ required for the Fibonacci construction; especially as the individual error of one ramulus has been found to range to 127° in the adult.

In the end, again, as in the Moss, one is inevitably led to the conclusion that the orientation of the lateral ramuli is not only within the control of the shoot as a whole, but that the details of apical-cell segmentation are subservient to this function, whether expressed in primary centric Fibonacci relations or in secondary bilateral symmetry. It may be noted that even with the best intentions one cannot fairly call such ramuli 'leaves', whether as elaborated frond-systems of species of *Sargassum*, or reduced to awl-like scales as in *Cystoseira ericoides*; dorsiventrality is wholly wanting and even bilaterality may be obscure, as such ramifications attain a more cladode-habit. But it now follows that the Fibonacci system of organization is older than the attainment of the 'leaf' as understood in sub-aerial vegetation, and is a phenomenon of response to conditions of marine environment; so far beyond the horizon of all land-vegetation, and only surviving in the latter as a part of the inherited equipment of the sea; though further specialized and utilized as it proves efficient under new conditions of sub-aerial progression.

VIII

QUINQUELOCULINA

ONCE it becomes clear that Fibonacci symmetry in the production of lateral appendages of a main axis, in acropetal, spiral succession is a phenomenon general among more massive marine Algae, as the response to a condition of submarine environment, the story of phyllotaxis takes a new turn; since it is obvious that the presentation of Fibonacci factors in the case of subaerial vegetation can be only interpreted as the retention of an ancient mechanism, adapted now, it may be, to the insistence of problems of insolation on land, but of undoubted primary relation to a wholly different set of physical conditions; yet so deeply impressed that it is retained more or less clearly for all time in transmigrant vegetation. Similarly it now becomes of interest to look in other directions for any comparable illustration of the same general principles, which may afford a guide to the more deep-seated and fundamental factor involved. Such a clue may be possibly found in a race of entirely different organism, the Foraminifera, as a heterotrophic, holozoic, animal phylum of Protozoa, without chloroplasts, and with no photosynthetic problems, yet building in terms of a unicellular soma an organization which presents clear and definite factors of Fibonacci symmetry.

The attention of botanists to these remarkable little organisms, both living and fossil, was first drawn by Van Iterson (Delft, 1907), and many figures from zoological and geological works of Munier-Chalmas and Schlumberger are given in his work on Blattstellungen.¹ Obvious Fibonacci constructions are presented in such types as *Quinqueloculina vulgaris*, *Triloculina rotunda*, *Periloculina Raincourtii*, *Pentellina Douvillei*.² Forms are also found in which juvenile centric organization grades into bilaterality in the adult (*Heterillina Guespellensis*),³ as other types express strict bilaterality from the first. Other variants may be symmetrically 2-spined, or even 3-spined in the manner of the *Polytrichum* bundle-traces; cf. *Spiroloculina*, *Idalina antiqua*, and *Trillina Howchini*, Schlumberger (1893). The Fibonacci construction among such types is but one out of many possible systems; though generally accepted as the optimum and so far the highest expressions of somatic specialization.

It remains to analyse the factors of the growth of such organism, and to discuss the special value of the phenomena observed. Preparations from geological or zoological works, or from sections of decalcified material, are less satisfactory, as being doubtfully expressed in exact measurement. Yet Iterson (p. 311, loc. cit.) gives, for *Pentellina Douvillei*, a series of 10 successive divergence-angles, as 143°, 140°, 127°, 152°, 127°, 135°, 142°, 128°, 147°, 134°. The extreme range from 127° to 152° again gives a wide latitude; but so far the average works out as 137.5°, which leaves the matter sufficiently suggestive as a phenomenon undoubtedly expressed in terms of the same general Fibonacci category, and requiring further examination. An illustration of a transverse section of *Quinqueloculina seminulum*, figured by Worth (1907) in the Journ. M. B. A., appeared so beautifully cut and symmetrical that it might be taken as a type (Fig. XIII).

¹ Van Iterson, jun. (1907), 'Mathematische und mikroskopisch-anatomische Studien über Blattstellungen', p. 299.

² Van Iterson, loc. cit., p. 306.

³ Cf. *Biloculina depressa*, Minchin, (1912) Protozoa, p. 233.

Quinqueloculina (Miliolina) seminulum,¹ L., a universal and cosmopolitan Foraminifer of benthic habit, with calcareous test about 1 mm. in length, is common in every latitude from arctic seas to the equator, and from shallow water to 3,000 fathoms (as tests only). It is also geologically recognized in the Eocene, and in all deposits since ('Challenger' Rep., 1884, p. 160). It is generally regarded as a type of the leading and most highly successful forms of Foraminifer. The special nature of the construction is not particularly obvious from external view; the organism appearing as a cluster of arching tubules or chambers, convex peripherally, with oral aperture and plasmatic web of pseudopodia. A transverse section half-way up the length gives the optimum effect. The specimen figured was just over 1 mm. diam., and, though damaged peripherally, showed about 20 chambers, the majority being perfectly defined. It occurred in a pebble of Eocene limestone, dredged 38.8 miles S. 11° W. of the Eddystone, and belongs to a collection of the rocks of the district. The slide was kindly lent by Mr. R. H. Worth of Plymouth for the purpose of making the figure. A large camera lucida drawing, under the high power, a foot in diameter, showed up the minor errors of the construction, and permitted the measurement of the angles with considerable reliability, as in a phylogenetic construction. The organism apparently sank with vertical orientation, and the pebble-section followed a horizontal plane with utmost accuracy.

The figure clearly shows that while the outline of the new chamber is founded on the 'quasi-square', with minor sculptural variations; the cavity of each is theoretically circular, being equally clearly a retardation-derivative of a quasi-circle, and bilaterally symmetrical in the plane of section with regard to a radius of the system as indicated by the dotted lines used for measuring the divergence-angles. Extreme flattening obtains in the more peripheral chambers, but at the optimum region of the construction (Nos. 6-12), the effect of both quasi-squares and quasi-circles is the most remarkable and most critical feature of the system. It may be also noted that the general distinction between 'three-rowed' *Triloculina* and 'five-rowed' *Quinqueloculina*, is merely the expansion of the amount of tangential extension in the units, and has nothing to do with the Fibonacci angle. Extreme tangential extension leads on to the assumption of bilaterality only, as in *Biloculina*, *Spiroculina*. To any botanist the figure is a good example of a 'bud'-section.

Examination of the outermost chambers shows minor inequalities, as some of these encroach beyond their legitimate territory, and the individual form varies somewhat towards the periphery, with more elaborate sculpturing of the outer margin of the test, 2-, 3-, 4-, 5-ridged, while the peripheral members appear more tangentially extended or flattened. These details express the general plan of growth in adding new chambers to the test *one at a time*, on a pre-existing base; general accuracy being maintained with remarkable perfection. The 'contact-parastichies' express a clearly-defined 2:3 system; the 'genetic spiral' can be traced on numbering up the areas in the usual way, and in this case it winds 'Right' from the centre outwards. The following divergences were measured on the plan, with accuracy well within the error of observation, just as in the transverse section of the *Sempervivum* apex:—

1-2	130°	7-8	145°	13-14	142°
2-3	156°	8-9	145°	14-15	152°
3-4	135°	9-10	141°	15-16	139°
4-5	151.5°	10-11	143°	16-17	14°
5-6	138°	11-12	140°	17-18	151°
6-7	142°	12-13	141°		

¹ Lankester (1903), 'Treatise on Zoology,' p. 83, described as presenting chambers on 5 radii, as it is formed by a rotation of $\frac{2}{3}$; cf. *Triloculina* and *Biloculina* (bilateral).

The range is again considerable (max. 156° —min. 129°), and the difficulty of accurate measurement is increased by the fact that there is no central point, as in the case of the central protoxylem of a leafy shoot: measurements are thus approximated. Even where accuracy was most attainable measurements did not come very exactly on the $137\frac{1}{2}^{\circ}$ mark, but rather average 140° ; but of the beauty of the system as a whole there can be no question. Taking averages of 5 successive members at a time, as a full cycle, to eliminate errors of centring (as in *Sempervivum*), successive averages range from 142° to 144.5° : the average of the entire sequence (18 members) was 142.8° ; a figure at first sight far removed from $137\frac{1}{2}^{\circ}$.¹

Perhaps the most striking feature of the construction is the exact radial orientation and consequent 'isophylly' of the loculi of the chambers, recalling the strict radial orientation of the derivatives of quasi-circles in an orthogonal construction; such a detail was quite unexpected, and is undoubtedly equally confirmatory of the fundamental mechanism behind the whole construction. There is thus no doubt whatever of the presentation in such an organism of *perfectly normal Fibonacci symmetry* in building the somatic chambers. The only questions are (1) How is it done, and what is the mechanism? (2) Why is it done? These problems being bound up with the organization of the Foraminifera as a class.²

The Foraminifera are to be regarded as a group of Protista, derived from an ancient pelagic flagellated series, residual traces of which are still retained in reproductive phases, as simple isokont or monokont (*Peneroplis*) zooids of the most elementary type. But with the assumption of a benthic and holozoic habit, nutrition is effected by means of a pseudopodial net catching plankton-rain of small dimensions (diatoms, &c.), the flagellated stage being suppressed in the adult; while the periphery of the soma is enclosed by a precipitated calcified test leaving an oral aperture (or others) for the extrusion of the net. In the case of regressive plankton-forms the test must act as a gas-holder for purposes of flotation, thus again replacing necessity for flagellar action (*Globigerina*). Where such food-supply is abundant and a substratum is available, a more benthic habit affords a satisfactory solution of the problem of nutrition, and such organism may attain considerable dimensions. But once confined by a rigid test, increasing growth is expressed in the production of new regions of similar form, similarly ultimately fixed by the calcareous deposit; the newer chamber being again usually larger than the preceding, though approximately of the same general

¹ By actual measurement the divergence angle is obviously fairly correct for the Archimedean angle 144° , and would be regarded as an unsatisfactory approximation to the theoretical log-spiral angle of $138^{\circ} 27' 42''$ (R.P.M.L., p. 340). Examination of the figure, however, shows that after the first few members the *radial depth* of the unit remains practically constant, and growth is adjusted in the tangential component. The log-spiral system implying uniform expansion of 'similar figures' is not maintained, and the Archimedean construction is the result of a secondary factor.

It is also interesting to compare the range of error in the case of the individual unit, as an amplitude of oscillation about the mean of 137.5° , in:—

<i>Quinqueloculina</i> . . .	$156^{\circ} - 129^{\circ}$.
<i>Pentellina</i> (Iterson) . .	$152^{\circ} - 127^{\circ}$.
<i>Cystoseira</i> (Fig. XVII) .	$154^{\circ} - 127^{\circ}$.
<i>Polytrichum</i> (Fig. XVI)	$152.5^{\circ} - 127.5^{\circ}$.

i.e. as much as 10 degrees either way: such a range of error at once eliminates all question of the necessity of working accurately even to degrees; as it also indicates the community of 'design' or 'response' in a wide range of organism in their relation to Fibonacci symmetry.

² Minchin (1912), 'Protozoa', p. 231.

Lankester (1903), 'Treatise on Zoology', i, p. 47.

Winter (1907), *Peneroplis*, A.P.K., x, p. 16.

Rhumbler (1903), A.P.K., p. 181: 1902, p. 252.

type. Different types of Foraminifera may be distinguished according to the characters of the complex soma thus built up; and the group apparently exhausts every possibility of spatial extension, as well as presenting a wide range of test from calcified shells to pseudomorphs of sand-grains, &c.: on the other hand 'naked' forms grade into other complex benthic and amebiform types of organism. As different phases of somatic extension may be distinguished,— (1) growth in a linear series, as extension in one dimension, *Nidularis*; (2) growth in a plane (two-dimensional) giving alternate chambers on the two sides of the original test, *Biloculina*; (3) formation of the new chamber always on the same side, with a bias, giving a winding helicoid coil, *Globigerina*, *Discorbina*, with the compactness of a snail-shell; (4) the most perfect construction for three-dimensional growth, from the standpoint of compactness of body, restriction of centric symmetry, and exposure of minimum surface of test, is clearly the Fibonacci construction, so long as only one new chamber can be built at one time. With this proviso, the Fibonacci angle of $137\frac{1}{2}^{\circ}$ is the mathematical solution of the problem, and it is interesting to find that it may be so readily approximated; while forms presenting such a construction are so far of distinctly higher grade.¹

The mechanism of the process appears fairly suggestive; given a plasmoid unit restricted to a definite form, building a second unit of similar form, the latter must necessarily fall on one side or the other (omitting the case of the linear series); and if the second unit remains in association with the first, with the same central control, the original centric equilibrium of the organism will be only regained as the third unit makes good the balance of the system; either falling at 180° from the second, giving the bilateral or two-dimensional condition, or balancing in the optimum three-dimensional position at $137\frac{1}{2}^{\circ}$, and so on in successive units. From such a standpoint, the 'balance' appears as another version of the general principle of growth in conflict with the demands of surface-tension in a fluid medium; and the fluid cytoplasm may be visualized as streaming automatically to the next position of 'balance', as inherited from a spheroidal phase, and being ultimately fixed by its deposit of metabolically precipitated excreta of calcium carbonate. In this way the utilization of the Fibonacci angle appears as a fundamental property of growing cytoplasm, confined within a rigid boundary, under the control of a secondary growth-factor which necessitates the building of new extensions of the soma *one at a time*. Of the possible solutions of this problem presented in different types of the Foraminifera, the Fibonacci system is clearly the best, as affording a compact unit which alone retains on the whole its centric symmetry in the optimum degree; i.e. so long as it follows the Fibonacci construction, it is constantly at the same degree of approximation to the radial condition. The conception of such automatic 'balancing', again, may be visualized as a mechanism which is so far unconscious, and beyond the immediate control of the organism. There is no need to postulate a conscious 'thinking out', or measuring the exact angle of $137^{\circ} 30' 20.9''$, a factor clearly beyond the capacity of any animal or any plant. But just as a man on a bicycle, when automatically balanced, is at an approximate angle of 90° with the surface of the ground, though never absolutely 90° (to the decimal of a second) for any conceivable space of time; so, when the plasma is automatically adjusted, as by the assistance of surface-tension acting on the plasma as a whole, the angle is equally approximated. There is no necessity to demand, or to be expected to demonstrate, the exact Fibonacci angle in any given case.² Given an inherited, or ingrained, centric or equalized

¹ Species of *Orbitolites*, by building radially many small alternating chambers as 'similar figures', many at one time, may present patterns at first sight closely comparable with the capitulum of Composites, though tending to equalized 'log-spiral parastichies'. Rhumbler, A.P.K., 1902, p. 249.

² This also explains at once why in the case of higher plants any pair of Fibonacci numbers from 2:3 onward will give equally satisfactory results, since in this ratio only is the error from $137\frac{1}{2}^{\circ}$ as much as one degree. (R.P.M.L., p. 340.)

and symmetrical growth-distribution, the angle follows; approximated on the whole, in the average of successive members around the centric field of growth, though with a possibly wide margin in the case of individual units, as these may vary in accordance with the interposition of a time-factor.¹ It further begins to be clear that what holds for the fluid plasma of a unicellular soma will equally hold for the plasma of a multicellular soma, similarly inheriting centric symmetry; just as the approximate cylindrical form of a tree-trunk is but the reflection in the massive soma of the primary claims of surface-tension, which gave centric form to the first passively suspended plankton-cells.

The essential point to note is the almost absurd manner in which the Fibonacci pattern of *Quinqueloculina* resembles that of a plant-apex, although the two constructions are worked out in *diametrically opposite terms*. Thus, *Quinqueloculina* builds one chamber at a time, placed on the *periphery* of the older test which is itself no longer growing: the effect of 'growth' and consequent log-spiral constructions will be merely the expression of the fact that successive units are *similar figures*, only differing in progressively increased dimensions. While in the case of the plant-apex, the new members are added one at a time *internally*, at the centre of construction of a growing system which is expanding throughout its entire mass; the log-spiral effect being again the result of the units remaining similar figures as they all continue to grow in graded sequence.

Only one factor is common to both,—*the building of new units one at a time,—and it thus appears that this is the essential factor behind all such presentation of Fibonacci relations, to all time*. Fibonacci symmetry is not only older than the 'leaf'; it traces back beyond the differentiation of stem and leaf, and is one of the most fundamental properties of living organism. Established in the working mechanism of a 'growing-point', itself the elaboration of the axes of benthic seaweeds, it is deeply ingrained in the constitution of all subaerial vegetation, and may be in turn one of the last factors to be lost in the general deterioration of apical mechanism. This applies with special emphasis to the case of floral shoots in which the mechanism of leaf-production fails as the flower attains a more finite and minimized organization.

As a secondary feature in which *Quinqueloculina* again comes into line with the spiral bud-systems of higher land-plants, may be noted the isomorphy (isophylly) of the respective units, as they present strict bilateral orientation with regard to *radii* of the centric system. Since such a property is apparently restricted to spiral constructions in terms of orthogonally intersecting log-spiral curves² (or legitimate derivatives from such a system by the addition of a new factor), it follows that in both cases the distribution of growth activity may be visualized as following the lines of physical forces acting in orthogonally intersecting planes, a factor common to other examples of distribution of 'equipotential', and so far a physical property of matter.³

By showing that a mechanism of strict Fibonacci symmetry is in practicable working order, even in a holozoic race of marine Protista, it is not intended to encourage any ridiculous idea that marine Algae must hence present some 'affinity' in these respects, or even may have had a common origin in some autotrophic organism similarly exhibiting such a growth-mechanism. Though it is quite obvious that countless races of Protista and low-grade Algae may have existed, and have been lost in the

¹ Hence in higher ratios accuracy will tend to increase as a larger number of units (typically a full contact-cycle) may be initiated practically simultaneously.

² R.P.M.L., loc. cit., p. 241.

³ Ibid., p. 230.

remote past, the fact remains, that among living vegetation of the sea, Fibonacci symmetry is first traced in parenchymatous massive growths of the Phaeophyceae, as it must also have been attained in equally parenchymatous massive marine Algae from which the higher vegetation of the land (Bryophyta, Pteridophyta, Phanerogams) has been derived.¹ The mechanism, that is to say, has been acquired polyphyletically as a consequence of the adaptation of a special mode of growth in very divergent groups, and it remains to analyse its significance still further. Taking *Quinqueloculina* as a guide, the production of one new chamber at a time represents a local extension of the somatic plasma, before it is fixed by the calcareous precipitate of the chamber-wall, and is so far a growth-thrust increasing the surface-area of the body, in opposition to surface-tension which tends to pull the organism into a state of minimum surface.² This is the essential clue to the situation. The phenomenon reduces to a special case of the original primary conflict between surface-tension of fluid plasma and plasmatic growth, which is the basis of all special form-factors. Every phylum of elementary organism, holophytic or holozoic, presents its own special solution of this problem. The case of the zoid with a unilateral extension, but no further development, is the first simple case to be discussed. The problem of the centric Diatom is much more elaborate, and affords the clue to a vast range of special somatic types of plant-nature. Beginning with a surface-tension sphere, the flattening of the soma to a circular disk expresses the restriction of growth in one dimension, but not in the other two. The meaning of the process is sufficiently clear; the centric Diatom, the discoid chloroplast of the autotrophic land-plant, and the discoid blood-corpuscle of higher animals, still express the retention of this simple phase of organism working in terms of surface-action. Beyond this stage, growth-thrusts, symmetrically spaced with geometrically balanced accuracy (as 2, *Navicula*, 3, *Triceratium*, 4, 5, 6, 8, 10, &c., of many Diatom-forms) afford a symmetrical (whorled) solution of the problem, fixed by a later deposit of silico-cellulose with almost mathematical accuracy. The points to note are,—(1) the growth-thrusts are equally distributed, more than one at a time; (2) they are initiated once for all: there is no possibility of further addition, and *the system is so far closed*; (3) they are orientated in one plane as a two-dimensional phenomenon.

From such a standpoint may be considered the example of one such thrust at a time, with the possibility of repetition; this is the case of the Foraminifer of the *Quinqueloculina* type. The factors being three-dimensional as,—(1) a longitudinal axis which is relatively unaffected, and (2) Fibonacci symmetry in the other two dimensions in a plane at right angles to the former.

That is to say, the Fibonacci symmetry is a two-dimensional function, and the solution of the problem of a growth-thrust in opposition to general surface-tension (though still working in terms of local surface-action), which now presents the additional possibility of being repeated, and so working out a growing pattern in an asymmetrical or 'spiral' sequence. It is this relation of symmetry, combined with the complete restriction of further growth, which is the essential factor dominating the progression of the Diatom-soma, and is also responsible for the circumscribed range of this otherwise remarkably kaleidoscopic form-series; as the symmetrical distribution of growth-form in dimensions at right angles to one another

¹ Church (1919), 'Thalassophyta', p. 96.

² Church (1919), 'Building of an Autotrophic Flagellate', p. 13.

expresses the fundamental claim of the general principles of orthogonal construction in living organism.

Any race of organism which thus combines growth in one longitudinal direction, as distinguished from the other two spatial dimensions, with growth in the latter at right angles to the first, distributed one member at a time, must inevitably, as the optimum solution of the surface-tension problem, work out a Fibonacci system in the plane transverse to the longitudinal axis. Because a benthic plant develops a longitudinal axis as its first asset in protobenthon of the sea, it follows that as soon as it builds lateral ramuli, one at a time, in rhythmic sequence, these should follow the Fibonacci rule. Observations of the somatic organization of Phaeophyceae and Bryophyta, show that this has been the case. It is now clear why phyllotaxis-phenomena are to be considered solely with reference to the transverse component of the apical growth-activities. The longitudinal extension of axial growth, which gives the 'spiral' appearance, is a compound factor which must be analysed into its orthogonal components. The higher plant retains in its organization this inherited response to asymmetrical growth, just as the cross-section of its main axis normally retains the transverse component of the older surface-tension sphere.

The case of a single growth-thrust from the unmodified sphere itself, followed by others at different points on the sphere-surface, is more complex, but is not known to occur in the plant-kingdom; it could only obtain in a suspended plankton-organism; hence its geometry need not be discussed. But simultaneous equal growth-thrusts, in three-dimensional distribution, afford the basis of the geometrical relations of the remarkable holozoic group of Radiolarian Protista. In the case of the holophytic plant this is again ruled out of the question; though whorled, symmetrical, and equal growth-thrusts are beautifully expressed in the apical construction of coenocytic Siphonae (*Neomeris*, *Dasycladus*, *Acetabularia*), without any necessary relation to antecedent spiral phases.

Fibonacci phyllotaxis, as a phase of plant-symmetry, thus reduces to a condition of centric, axial, growth-extension, combined with the out-thrust in rhythmic sequence of somatic protrusions ('ramuli') in the transverse plane. To maintain the older inherent centric organization, the Fibonacci angle, $137^{\circ} 30' 28''$, must be approximated every time, though the range of error may be considerable in the individual units. Actual measurements show that the general plan keeps very fairly adjusted in such divergent types as *Quinqueloculina*, *Cystoseira*, *Polytrichum*, and *Sempervivum*.

IX

PHYLETIC PROGRESSION IN PHYLLOTAXIS-MECHANISM

IN dealing with such a complex range of phenomena as that afforded by the phyllotaxis-relations of higher land-flora, one can only approach the subject from the standpoint of the land-plant itself, in its modern aspect; knowing quite well that such vegetation was never created directly for the position it now holds, but is the outcome of a long series of progressive adaptation; so that the modern equipment of a land-plant, though often apparently admirably suited for the necessities of its present environment,

must nevertheless have been initiated in response to a complex of entirely different stimuli. Every organism that exists at this stage of the world's history has been 'adapted', possibly, over and over again; and the object of scientific discussion will be to trace such adaptations to their final cause. Short-sighted sub-aerial teleology, which may attempt to find a solution in the more immediate claims of present environment, can never hope for any satisfactory conclusion, or meet with whole-hearted acceptance.

In analysing such a maze of component factors as presented by the relation of phyllotaxis-constructions to external conditions, it is first essential to trace backward, and to deduce from the material at our disposal (which may be quite imperfect) what can be so far definitely established as tending to the ultimate factors of causation, step by step; so that what is established from deductions afforded by the study of land-vegetation, and what is left still undecided, may be clearly distinguished.

I. It has been sufficiently demonstrated that all phyllotaxis-constructions, whatever, in higher plants, as phenomena of rhythmic production, can be readily discussed, scheduled, and figured, in terms of intersecting curves (the 'contact-parastichies'), and in no other way. This generalization applies equally to 'spiral', 'whorled', 'bijugate', and 'anomalous' systems, as also to cases of 'rising' and 'falling' phyllotaxis; and only fails in dealing with phases of ultimate deterioration, which present no system whatever, and thus can be scarcely considered as rhythmic, though vestiges of pattern may often remain.¹ There is no reason to suppose that complete absence of rhythm is the primitive case for any high-grade organism;² growing organism is presumably rhythmic, and the primitive laws of 'form' are not based so much on the irregular holozoic amoeba, as on the radiate symmetry of the surface-tension sphere of still earlier autotrophic organisms. It may be fairly concluded that such curves afford the best clue to the mechanism.³

II. The most striking and most constant feature of all such curve-systems is the fact of their 'concentrated' packing, in what was originally known as the 'quincuncial' arrangement of Bonnet and Calandrin, from the custom of planting in diagonal rows; so that phyllotaxis-systems give the effect of 'alternating' rather than superposed whorls or cycles, respectively. Exceptions to this mode of arrangement are so few,⁴ that the diagonally intersecting curves of the contact-parastichies may be undoubtedly accepted as the original lines of the general plan of the constructions.

III. Comparison of such 'diagonal systems' shows that the asymmetrical (or 'spiral') construction must be regarded as the primary case. The symmetrical ('whorled') homologue is less general, and where found is more characteristic of parts of the plant-soma which are either non-photosynthetic (floral-shoot), or it occurs in types of more xeromorphic habit, in which it has been teleologically identified with advantages of increased superposition and reduced transpiration. The primary mathematical case of asymmetry is thus confirmed as being undoubtedly the more general, and the systems of alternating whorls as special limiting cases, clearly expressing, by the retention of the diagonal construction-lines of a 'concentrated' plan, their derivative nature.⁵

¹ R.P.M.L., loc. cit., p. 220.

² Bower (1908), 'Origin of Land-Flora'; 'Strobilus-theory', pp. 441, 143.

³ 'Annals of Botany', xviii (1904), p. 233.

⁴ Cf. a few isolated examples of doubtful nature, in types with extreme xeromorphic organization; *Chirastrobilus* (Scott); *Alcismalryxanthomon* (sp.); Van Tieghem.

⁵ R.P.M.L., loc. cit., p. 142.

IV. Among the more primitive 'spiral' constructions, the great numerical preponderance of Fibonacci ratios shows that these must be taken as the more elementary, and most probably the original case. Exceptions commonly occur as simple factorial variants (bijugate systems, &c.), and the few 'anomalous' systems show simple divergence from the ϕ ratio of 1:1.618. All these latter again tend to approach this ratio as the systems rise higher in the numerical scale.¹ The extreme divergence of all 'spiral' systems lies between the ratio 1:1 and 1:2, with an optimum at $137\frac{1}{2}^\circ$; and all anomalous systems tend to approach nearer the 1:1 ratio of equality, rather than the 1:2 side of this 'ideal angle';² in no case passing beyond it. Thus, taking the possible combinations of the numerals 3 and 4—out of 3:3 (symmetrical), 3:4 (anomalous), 3:5 (Fibonacci), 3:6 (trijugate)—all occur: the same applies to 4:4 (whorled), 4:5 (anomalous), 4:6 (bijugate); but 4:7 does not occur, and 4:8 has not been recorded. The simplest anomalous cases 3:4 (cf. *Sedum*), and 4:5 (cf. *Lycopodium*), of the type $m:m+1$, are those found, and they are generally distributed. The fact that the Fibonacci relation is the commonest, most widely distributed, and therefore possibly the most primitive type, follows from purely morphological considerations, quite apart from any teleological explanation of its assumed advantage in the case of land-vegetation; as in the older views of Bonnet, which assumed optimum advantage for transpiration, or the later improved view of Wiesner that it gives the optimum angle for maximum exposure to light in photosynthesis.³ The latter standpoint covers and amplifies that of Bonnet; but it does not follow that even this view contains the whole truth, or is even near it. It still remains to explain (1) How the plant ever found the angle, (2) The original mechanism of production; and the conclusion is immediately suggested that, even for purposes of photosynthesis, the construction-system has been 'adapted', and there may be still something behind.

V. But having got thus far, one can look back and see the vast range of secondary phenomena covered by 'compromises' between positions of 'maximum exposure' and 'minimum exposure' (superposition), which make up the systems of the leafy-shoots of land-plants; as also the remarkable fact that the most perfect expressions of Fibonacci-relations, and again the most constant in occurrence, are always to be found, not in the more perfectly equipped photosynthetic shoot-systems, but in constructions in which the demand for photosynthetic exposure is *nil*; e.g. in the scales of Conifer cones, the inflorescence-capitula with generally suppressed 'bracts' of Composites, and the stems of leafless Cacti. The conclusion is forced upon one that there must be after all some further object in view, as the expression of some still more fundamental law of living organism, of which leaf-arrangement is but one special case. The only satisfactory generalization behind the utilization of the Fibonacci ratio in land-plants is that if the plant for some reason 'prefers' or is bound to build one new member at a time, the Fibonacci angle is undoubtedly the one to approximate. But there is no apparent reason so far put forward as to why the land-plant should be so handicapped. Examples of whorled systems, and their mechanism for the production of members simultaneously, show that this can be done with equal facility; yet whorled systems appear as an

¹ R.P.M.L., loc. cit., p. 72.

² loc. cit., p. 197.

³ Little better than the original view of Leonardo da Vinci; cf. Cook (1914), 'The Curves of Life', p. 81.

afterthought. It can be only concluded that the plant is somehow biased from the first in favour of members arranged one by one in a Fibonacci sequence; and the suggestion immediately offers that this may be in some way the expression of the inheritance of the equipment of a preceding phase and the solution of a much older problem.

VI. The case of the Moss-gametophyte, in which a similar result is worked out apparently as the effect of a segmenting 3-sided apical cell—though more probably, since the segmentation-planes are otherwise unaccountably oblique, only associated with such an anatomical mechanism—affords the connecting link with still lower races of organism within the submerged environment of the sea, in which all the phenomena of space-relations similarly obtain; though no horizontally extended photosynthetic laminae demanding exposure to vertical light are in existence, or have been as yet evolved. The seaweed (as expressed in the Fucoid alliance) is equally under the necessity of building one lateral member at a time (though, in this case an obvious 'branch'-ramulus, rather than a highly-specialized 'leaf'-member), and the same consequences of Fibonacci orientation are to be observed. Whether the mechanism of production is, or is not, associated with the nuclear mechanism of apical-cell segmentation, is clearly immaterial. The system is undoubtedly capable of secondary adjustment (as in the bilateral *Halidrys*), whatever may be the angle given by the rotating nuclear spindle of the apical cell. Finally the case of the leafless seaweed is extended to the limiting expression of the holocytic Foraminifer, in which light-effect is completely ruled out of the problem; and in terms of an entirely different, or even diametrically opposed mode of growth, the same Fibonacci result follows, even with recognizably equal accuracy.

VII. The last case gives the conclusion needed, that it is the necessity for building one member at a time (whatever the 'member' may be, that is the significant factor, to which all others are secondary and subsidiary. The question of Fibonacci orientation thus reduces to a function of primary centric growth correlated with secondary asymmetrical increase in a plasmic mass, within the operation of surface-tension, and so reduces in the limit to the fundamental problem of the struggle of living fluid organism, working in terms of surface-exposure to the medium of the sea, to maintain something more than minimum surface.¹ If in such a plasmic and plastic organism, outgrowth in one direction is followed by a compensating growth-movement in the next position for balanced equilibrium, the attainment of the latter implies the presentation of a 'divergence-angle' ($157\frac{1}{2}^\circ$) of the Fibonacci series, as an inevitable consequence. The repetition of the growth-movement works out the Fibonacci-pattern, as a construction alternative to the symmetrically placed growth-extensions of many centric Diatoms, the helicoid spiral of other Foraminifera, or simple 'bilateral' oscillation in one plane. The special advantages of the Fibonacci rhythm being (1) the maximum compactness of the resultant soma, and (2) its capacity for *indefinite growth-extension on the same terms*.

With this fundamental generalization at last attained as bottom-ground on which to build, it is possible to begin to reconstruct the progression of such organism along its upward path. In the lowest massive growths of multiseptate phytobenthon of the sea, the necessity for increasing the body-surface by *ramification*, follows as the natural response to the conditions of the moving medium, in which the main axis requires to be mechanically adjusted to resist the strain of wave-tension. Such primary ramification increases the somatic form along similar lines, and may be wholly irregular.

¹ Bot. Mem. 1, loc. cit., p. 11.

Any point of the surface may 'throw out' a new branch, exactly as any part of a benthic amoeba may throw out a local 'pseudopodium'. Examples of such elementary benthic growth-forms are common to the present day in simpler Phaeophyceae (cf. *Mesogloia*), and are also abundant among Florideae, traced in the isolated flagellate progression of *Hydrurus*, and the case of the *Schizoneima*-Diatom. The last vestige of such archaic irregular ramification may be traced in higher land-vegetation as the 'adventitious branch' or even root. But with the progression of phyto-benthon to more localized and apical growth in the main axis, ramification becomes increasingly restricted to the distal or apical region of the shoot; the adventitious character is diminished and finally suppressed, as the older portions in attaining an adult-phase lose the capacity for initiating new and young growths. As again, taking well-known examples in the case of higher vegetation, the retention of pericyclic tissue in a permanently juvenile condition renders possible the production of adventitious roots, and wound-callus may regenerate either new stem or new root-apices. In all such cases the primary irregularity of ramification settles down to the production of individual ramuli one at a time, in acropetal series; and the necessity for equal-spacing, as a balancing of the symmetry of the shoot, follows as naturally as the retention of its radial organization and cylindrical form. Still more perfectly can such a mechanism be established when the segmentation of the apex itself, within the control of a single dominant apical cell, acquires precision in the centric distribution of the growth-forces. But it remains abundantly clear that the possibilities of Fibonacci orientation in the branch-ramuli are older than such specialized apical differentiation, as they are far older than the differentiation of even leaf-laminae. Fibonacci symmetry is, in fact, one of the most archaic of somatic factors; it is difficult to trace anything phyletically more remote. This, again, undoubtedly affords the clue to its extreme persistence, even when no longer an integral part of shoot-construction; e.g. the retention of a complex mechanism for the distribution of groups of spines on a leafless *Cactus*, or the predominant retention of the number 5 in whorled petaloid flowers. While the case of the Moss now appears as a joint association of the apical mechanism of cell-differentiation with the Fibonacci orientation of more definite leaf-laminae,—to the extent that the latter is quite as possibly the causal factor, in the presentation of the limiting case of the 3-sided centric apical cell, as the more obvious mechanism of the cell itself,—the obvious dissociation of the two factors in the Pteridophyta only amplifies the story of the Furoid; and henceforward there is no doubt whatever that these two functions of a growing-apex are entirely independent of one another. The case of *Equisetum* remains to make this perfectly clear.¹ On the other hand, in the case of higher plants, it is evident that there must be some new apical mechanism of control, which involves the working out of such perfect patterns. So long as the numerical expression of these ratios remains low, the appearance of building one member at a time works out as the familiar 'genetic spiral'-effect of the adult shoot-system. But with numerical increase of the ratios, as the effect of a diminished diameter of the lateral centres in comparison with the diameter of the axis, many members are being formed practically simultaneously (e.g. scores in the case of a Composite capitulum, or even hundreds in the classical example of the great Sunflower heads, working in terms of 89:144, at least a full contact-cycle arise simultaneously, so far as can be seen), and the 'genetic spiral' appears as a useless abstraction. At such a stage it now becomes

¹ R.P.M.L., loc. cit., p. 150.

obvious that the mechanism, having lost its initial factor and intention, may begin to become irregular and anomalous; and hence it is in floral constructions involving small reproductive members of no photosynthetic value, that the system begins to break down; as in the gynoceum of the Strawberry, the sporophylls of *Clematis*, or the androecium of the Poppy. These last become familiar examples of sheerly irregular systems, with only vestigial rhythmic effects; both the idea of one member at a time and that of Fibonacci symmetry being hopelessly lost, nothing is left but a vague acropetal sequence. Even this is open to alteration, as in the example of the androecium of the Paeony. Finally, by loss of all construction-factors the shoot-system returns to an almost algal-like phase of indefinite 'enations', as postulated in conventional strobiloid theory.

At this point one is again brought up against the fact that the parastichy-curves are the only constant and fundamental feature of the constructions. All irregularities in the system reduce to variations in the numerical constants; and, bearing in mind the fact that the isophylly of the primordia, as expressed in quasi-circle origin, postulates an orthogonally segmented system, one is driven to the conclusion, *whether one likes it or not*, that the apex presents a certain capacity for numerical choice in the numerical expression of certain intersecting paths of equal distribution of the growth-forces which may be included within the convention of equipotential. The ingrained habit of building one member at a time, inherited from the benthic seaweed, remains curiously dominant even in land-vegetation of the highest grade; yet at any time the claims of balanced symmetry may light on the simple solution of the problem, as expressed in building several members simultaneously with mathematical precision, from the horizon of *Equisetum* onwards; though only in the most advanced types of photosynthetic reproductive shoots (decussate and distichous types) can it be said to become at all general. Only, again, in the non-photosynthetic reproductive shoots, as the sporophyll-region of higher flowers, does it attain any conspicuous degree of predominance, and in a manner which on any other causal or merely teleological interpretation remains wholly unsatisfactory and even unintelligible. Thus in a simple flower, as a Rose or a Geranium, the retention of a quincuncial calyx in the floral organization presents the last obvious relic of a mode of growth older than the first evolution of the foliage-leaf, of which the sepals are but the deteriorated expressions; as again the accurately whorled and alternating condition of the stamens in a Columbine or a Geranium could have been only attained in virtue of such primary and ancient equipment. It is the possibility of thus referring even minute and apparently trivial, or wholly meaningless and otherwise unintelligible, details of the organization of modern flowering plants to the remotest epoch of the progression of the vegetation of the sea, that renders such morphological investigations of supreme importance in attempting to gain a vision of the distant vistas of the progressions of plant-life in full and correct perspective.

There can be no doubt that in the consideration of the progression of plant-life from the antecedent phases of plankton and benthic existence, one does begin to obtain a glimpse of the manner in which one of the most fundamental principles of somatic organization has been evolved. The morphological construction which is destined to prevail as the most successful method of initiating new extensions, as ramification (or 'segmentation') of the soma, to be ultimately co-ordinated with the primary 'axial' region as 'appendages' of special function, gradually changes its mechanism of production, in terms of advancing anatomical organization, although retaining a closely identical morphological expression. From the condition of

the unicellular soma, the mechanism is traced to the benthic alga, ultimately with multiseptate axis and a segmenting apical cell, to still more massive growths in which the apical cell loses its domination, to be replaced by more obscure growth-processes with apical control; the latter appearing at the apex of the land-plant, in which the member-producing function of the apical cell is entirely superseded, though the construction still retains in all essentials its Fibonacci symmetry (Filicineae), or a special case of symmetry readily derivative from these relations (*Equisetum*), together with many variants and decadent stages (Filicineae, Lycopodineae). The initiation of the primary ramuli (now distinguished as leaf-appendages) follows a third method of production, and this mechanism remains as the characteristic expression of all higher plant-forms. One may not yet see exactly how it is done, as a more intimate plasmic or even 'molecular' function, and the equipotential theory so far is helpful as covering all the facts of observation; but that phyllotaxis-mechanism has passed through successive phases of evolutionary progression,¹ and is by no means to be explained by subaerial botanists as a condition of casual adaptation to the state of the plant as now found growing on the land-surface, much less to be lightly interpreted along teleological lines of the modern world,² appears at present the surest foundation on which to erect hypotheses of the evolution of what is termed 'stem' and 'leaf'. Academic abstractions of 'caulome' and 'phyllome' are meaningless expressions in view of the broader outlook which demands some definite information as to why a plant is what it is, in terms of cells, tissues, members, and space-form.

Taking the general progression of Fibonacci phyllotaxis as the expression of an archaic method of initiating one lateral extension of the soma at a time, from a growth-centre or a differentiated growing-point,—a process which may be continued indefinitely with optimum, self-regulated, balanced symmetry, undoubtedly on the whole the most satisfactory solution of the problem of indefinitely continued two-dimensional extension—the more fundamental and primary relations of living plasma, established once for all, even in the plankton-phase, may remain predominant, with little or no change, throughout all future phases of progression, as if their value might not be questioned. This has been seen to apply to the photosynthetic

¹ Centric symmetry may be said to characterize Coelenterata, as bilateral and dorsiventral symmetry prevails in all phyla of originally creeping and benthic Metazoa; centric *asymmetry*, inevitably involving Fibonacci-relations, dominates the plant-kingdom; other phases of symmetry (whorled and dorsiventral), being of secondary significance only. Spiral effects are equally secondary or subjective, as Fibonacci symmetry is seen to be the expression of an oscillatory balancing effect in two dimensions. All phases of somatic symmetry date to the earliest benthic forms in which elaborate somatic organization was first evolved; the main groups of organisms diverging along their special lines, the more widely as subaerial transmigrants.

² Analogies are not wanting in other departments of biology; for example, a man's nose, with distinctly heritable minor details, is derived from the pointed end of the body of a benthic fish; the latter expresses the pointed end of a flagellate, overhanging the primary oral aperture (cytostome), in turn the consequence of a phase of elementary polarity beyond the original surface-tension sphere of aqueous plasma, and so far tracing back to phenomena associated with surface-tension. Yet few would suggest that the nose is modelled in the human embryo, at the present time, solely as a result of surface-tension. As the organism becomes more complex, so the mechanism producing it may be elaborated beyond recognition, or new mechanism may replace the old; such mechanism being not only individual but racial; i. e. representing inherited response to conditions possibly no longer effective.

mechanism of the chloroplasts of early autotrophic flagellates, apparently little changed in the vegetation of the land to-day; the evolution of the nucleated cell as the plankton-soma, still the unit of all higher structure, plant and animal; as also to the fundamental organization of the multi-septate axis of incipient phytobenthon, with its capacity for indefinite ramification and ultimate delimitation of a growing-apex. The more fundamental the construction-factors of the more massive plant-soma, as solving the first problems of benthic existence, the more ingrained do they appear in the structural mechanism of the race for all future time, and the more difficult to eradicate. Few more striking illustrations in plant-morphology are available than the retention of precise phyllotaxis-constructions in such a group as the Cactaceae, where photosynthetic leaves have been practically entirely suppressed; in fact if the majority of phyla of Land-Flora had so happened to follow the vegetative organization of this small xerophytic series, we should have heard little about spiral phyllotaxis being the solution of the problem of optimum distribution of leaves to incident light. The occurrence of Fibonacci ratios in plant-organization, originally the expression of balanced symmetry within certain limitations, thus persists to the present day throughout the great range of modern land-flora; and on the whole proves equally satisfactory as applied to the problems of spatial distribution and light-utilization. Though by no means the only solution possible, it happens to be the one given by inheritance from previous phylogenetic phases, and hence remains largely unaffected in the great majority of land-phyla; compensatory corrections may be added in terms of other secondary growth-phenomena. Only in the general case of increasingly complex floral organization, can an attainment of secondary whorled symmetry be said to be at all characteristic; and in this case, again, it is practically confined to the sporophylls as reproductive members. Hence in higher petaloid flowers the change is associated with the localization of sterilized 'corolla'-members (Dicots.), or involves members of the perianth (Monocots.); while the calyx (perianth), itself vestigial, retains with wonderful conservatism, otherwise wholly unintelligible, indications of its Fibonacci origin; even in many cases (whole families) in which the phyllotaxis of the vegetative shoot may have been similarly changed to symmetrical construction (e.g. 2 : 2, or decussate), as in pentamerous flowers of Labiatae, Gentianaceae, Loganiaceae, Apocynaceae, &c.

The futility of attempting to reach a final solution of such problems, by mere observation of the mutual relations of the lateral photosynthetic appendages of transmigrant Land-Flora, may be now admitted. All primary structural relations trace back to the sea. The solution of primary problems of stem and root, leaf and branch, members and tissues, cells and space-form, is to be sought far behind the comparatively modern and woody secondary subaerial environment in which we find ourselves and the more familiar vegetation of the land. That early botanical writers lived in ignorance of this fact excuses their many limitations; at the present day a much broader perception is possible, and with the opening up of the indefinite vistas of life on this world, as a cooling planet, much of the older and more academic outlook requires re-orientation. To many botanists this sort of general conclusion may still appear fantastic, as savouring of 'Nature-Philosophy'; but it may be pointed out that the 'Nature' of the biologist, by which may be understood the progression of life on this world, is a very real phenomenon, still demanding a philosophy for its interpretation and presentation, as well as encouraging the mere accumulation of isolated facts.

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FIG. V. Transformation of (5:5) to eccentric homologue (zygomorphic pentamery).

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C_1, C_2, C_3, C_4, C_5 , the centres of construction, and O_3, O_4, O_5 , the origins for respective curves.

A circle AB with centre C , has been drawn in contact with the (3:5) curve for purposes of comparison.

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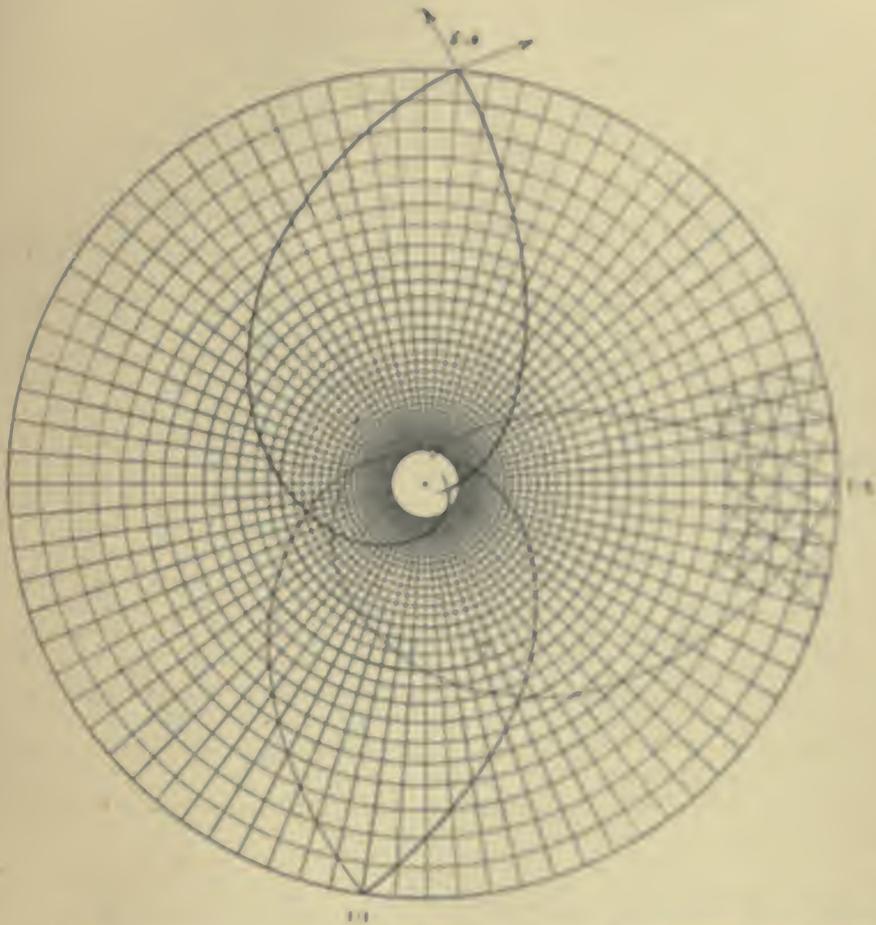


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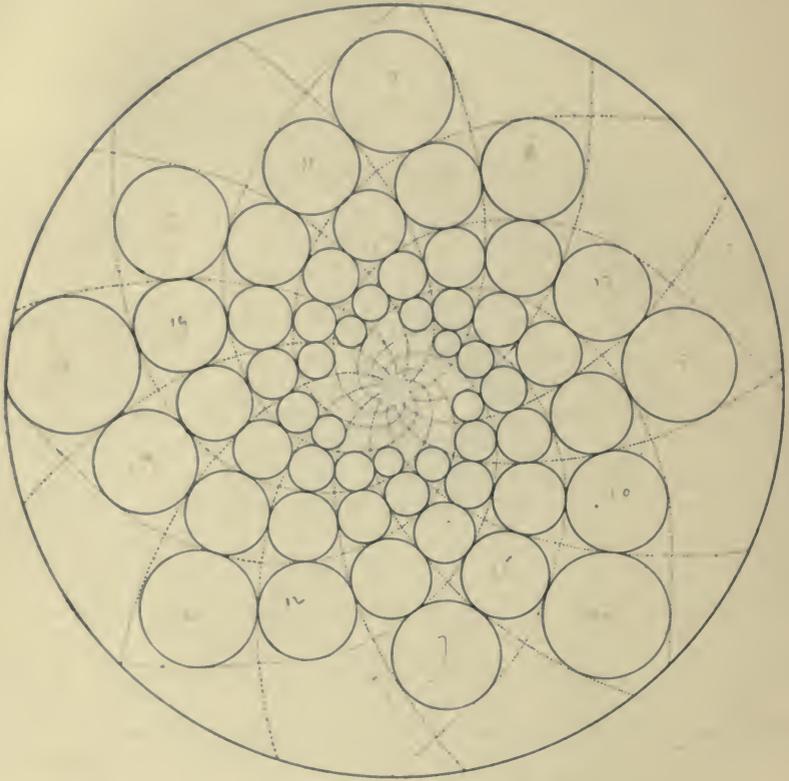


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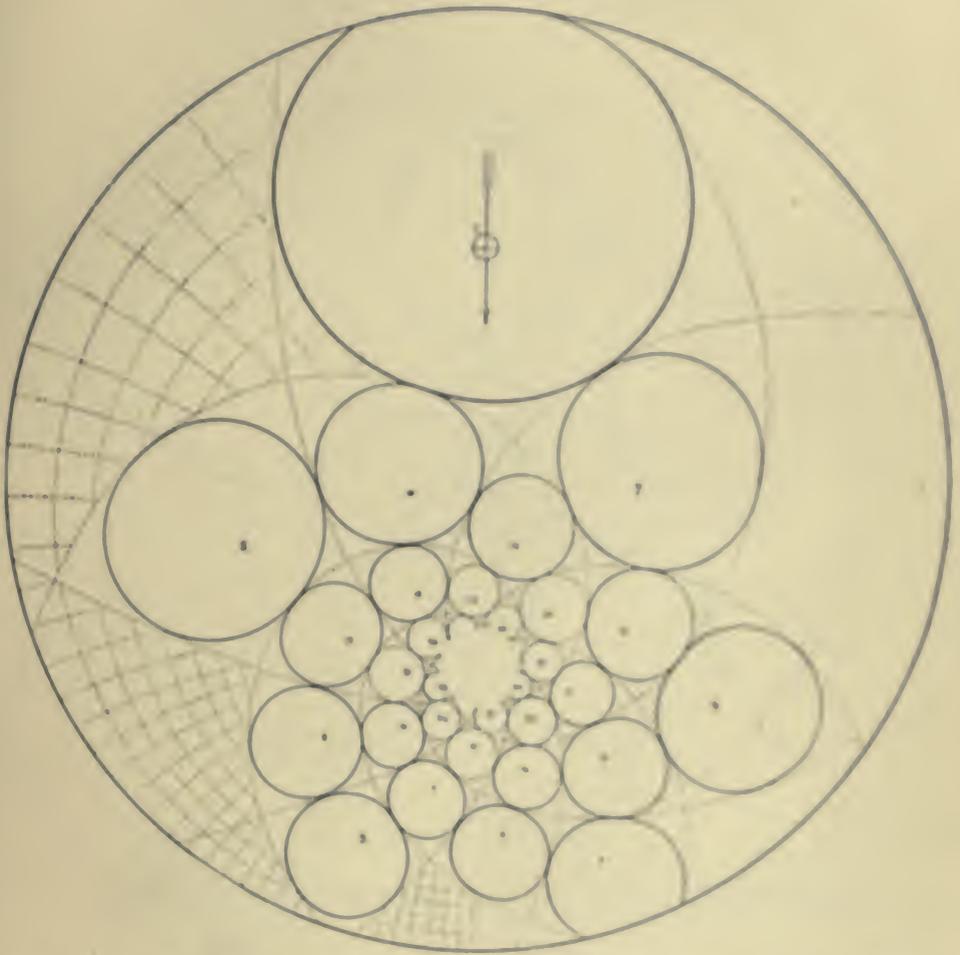


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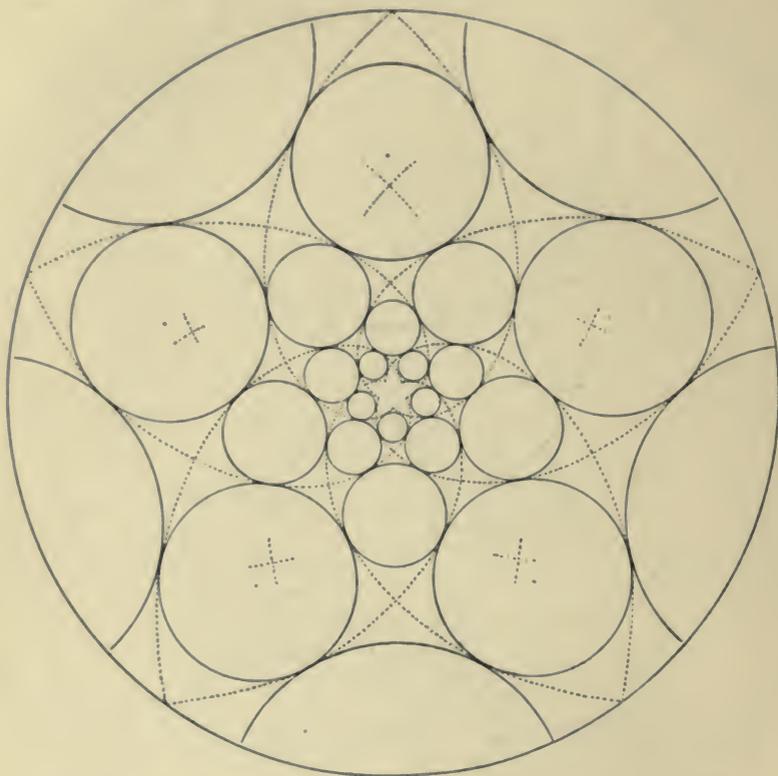


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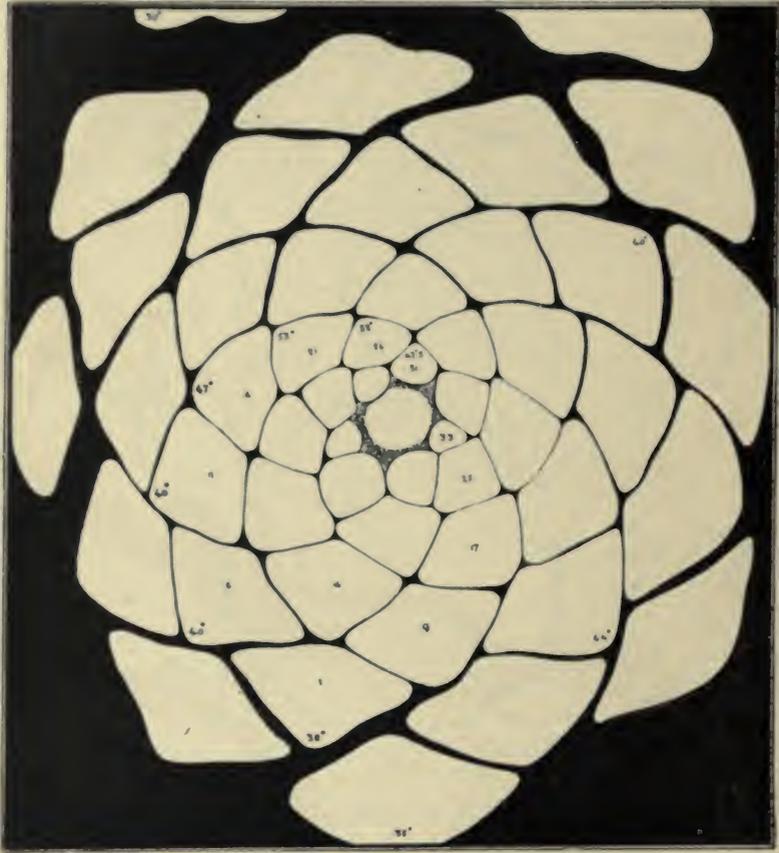


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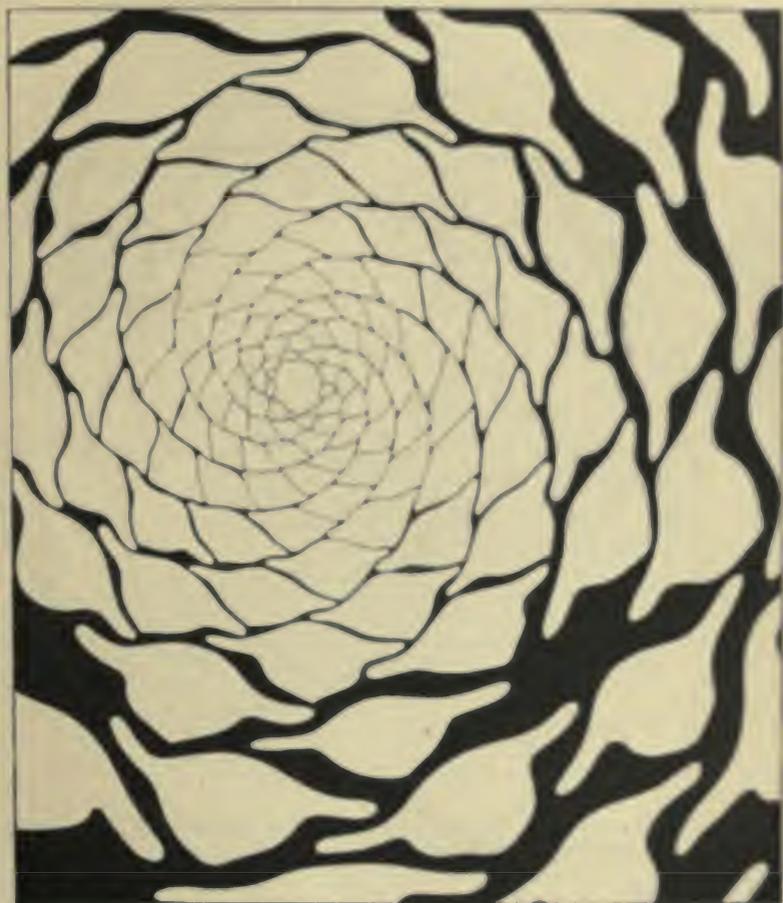


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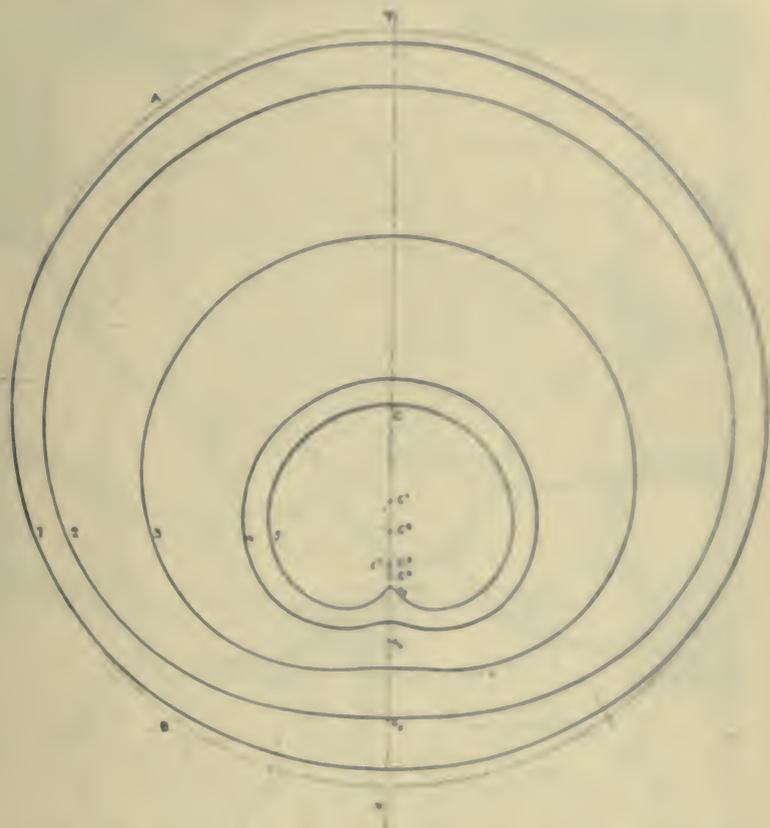


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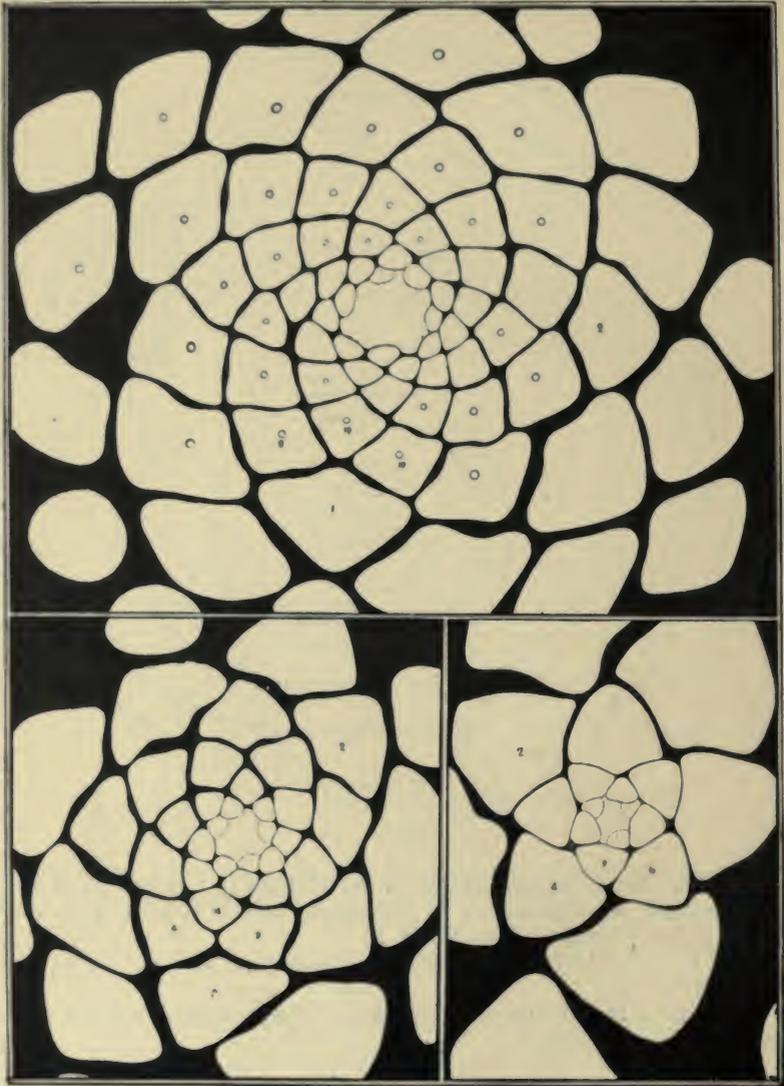


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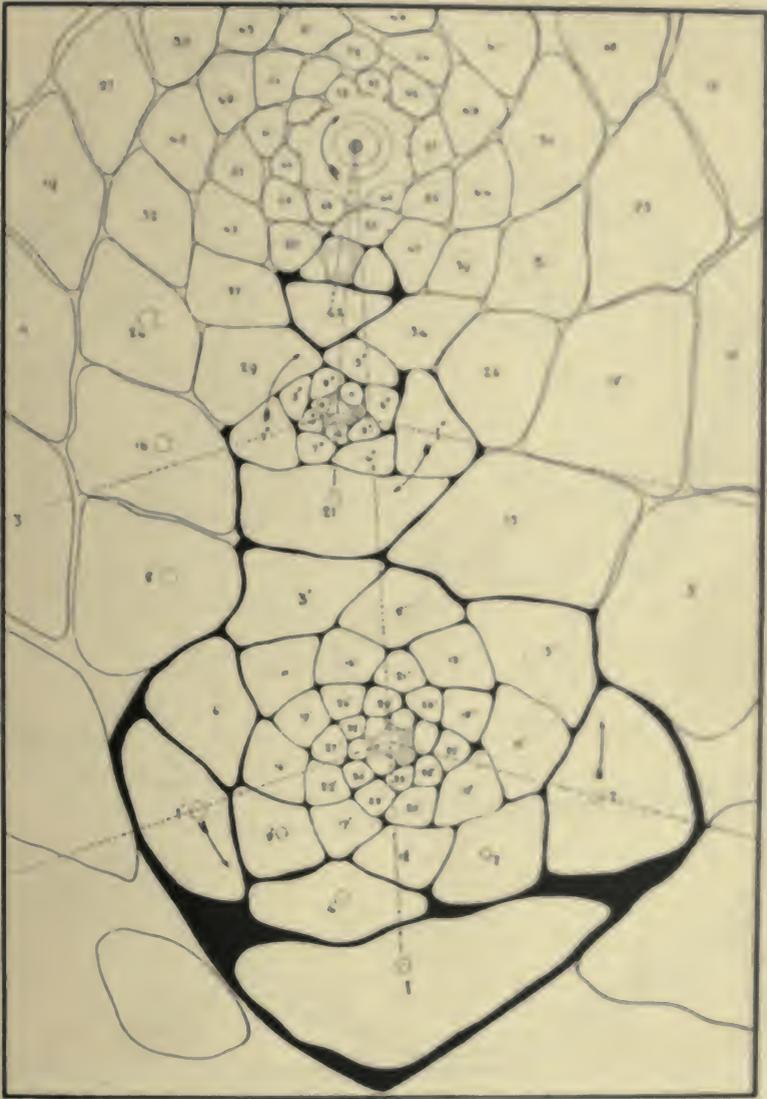


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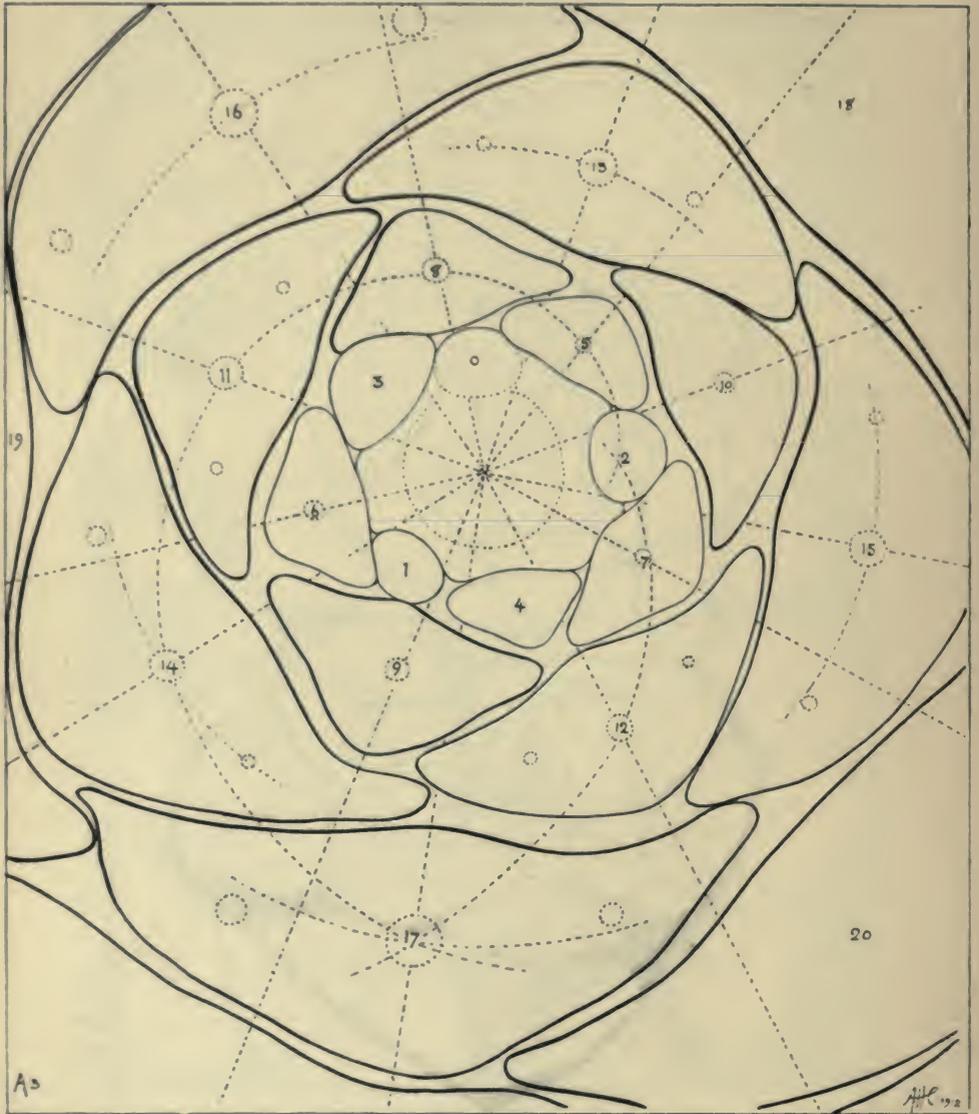


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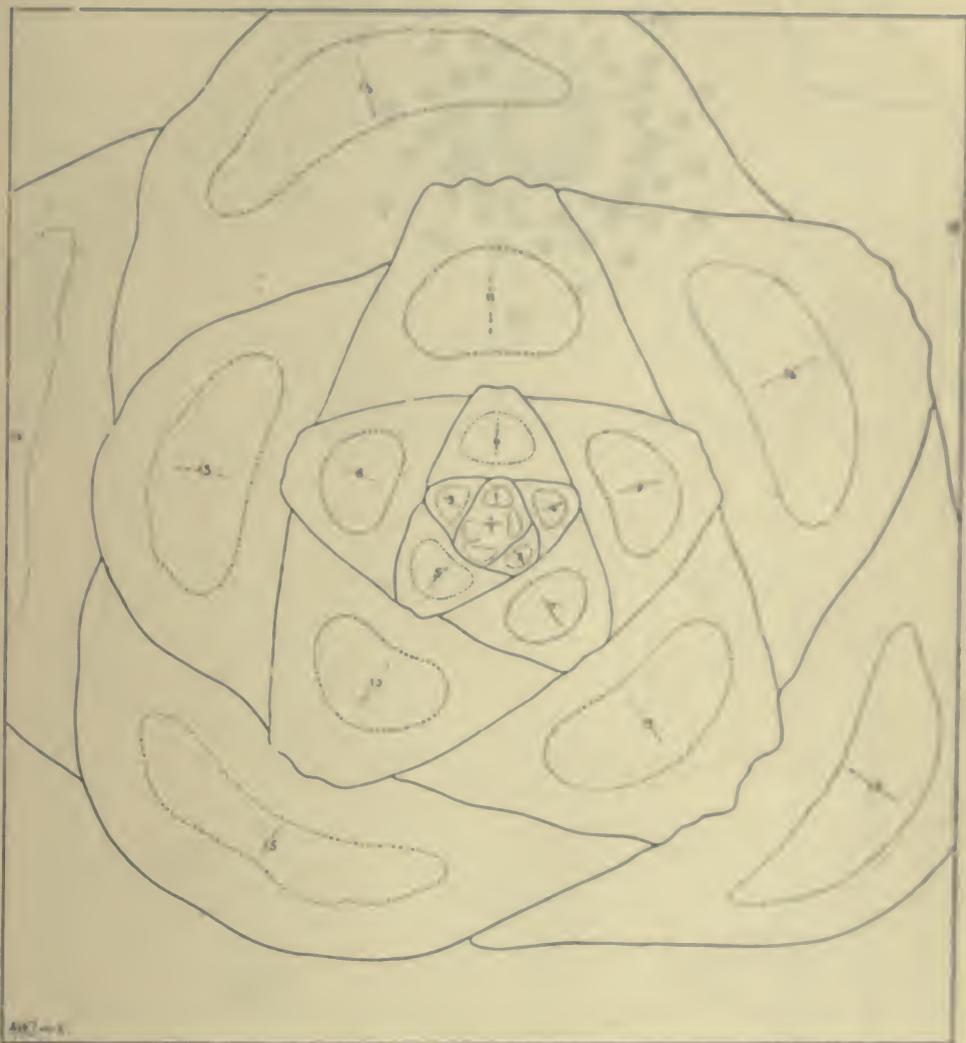


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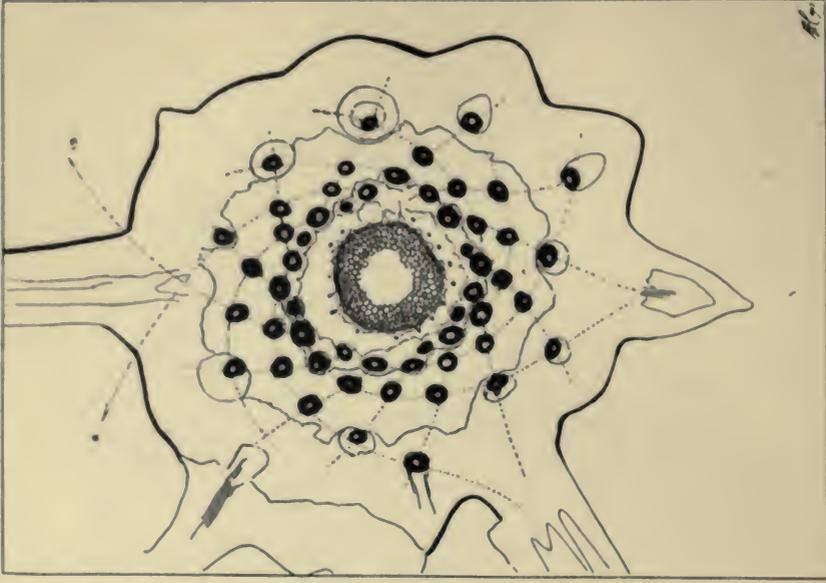


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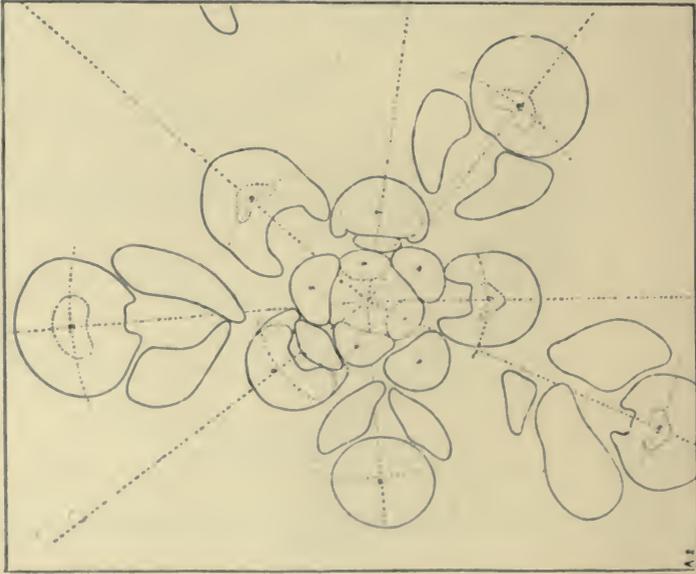


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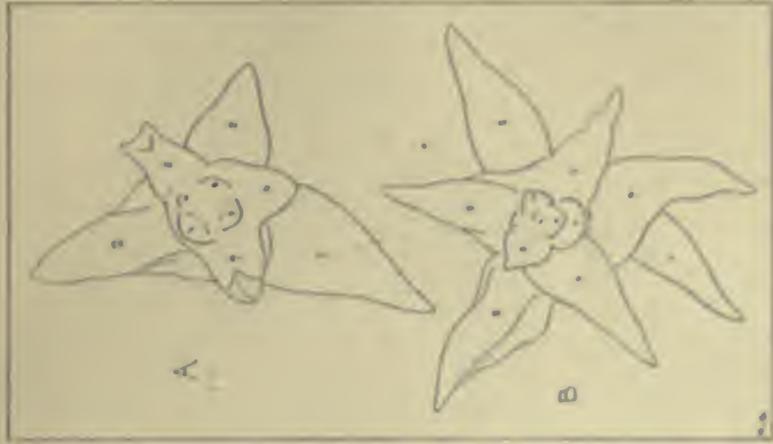


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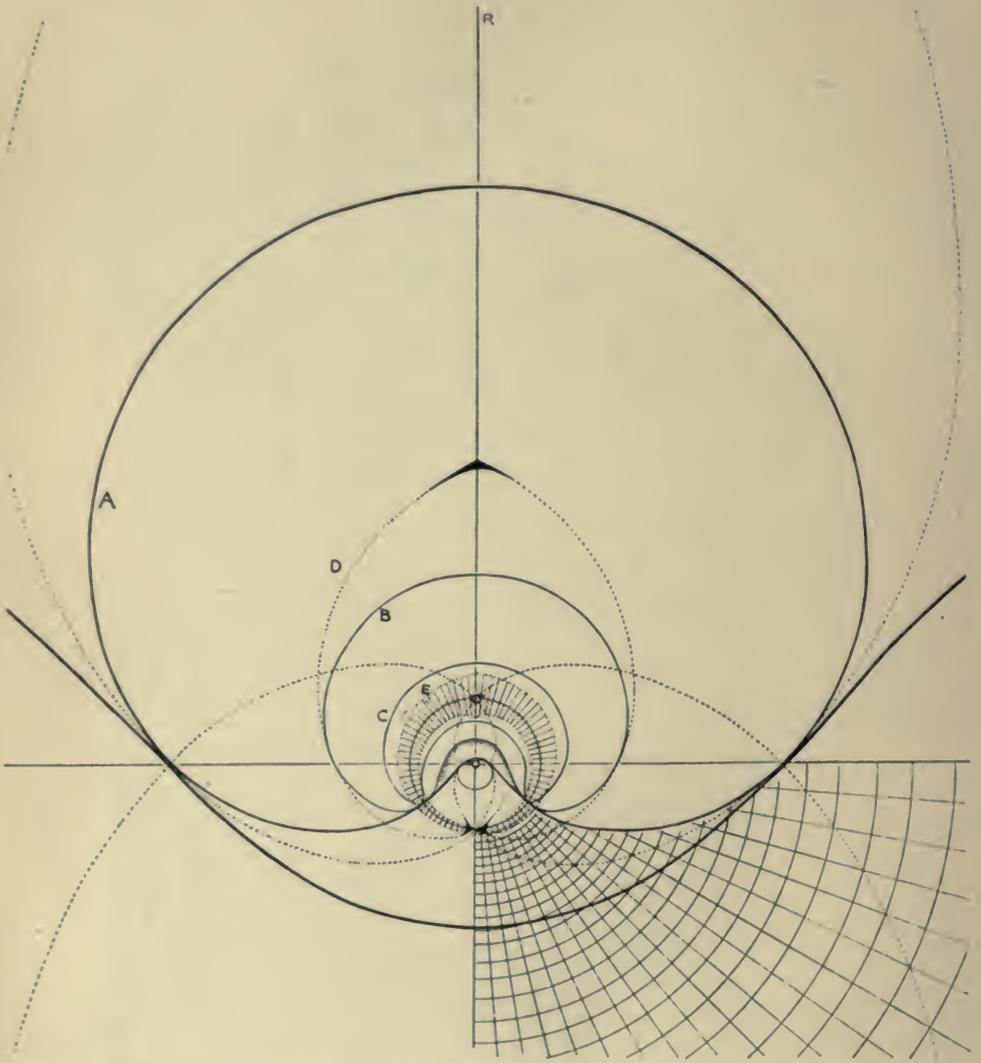
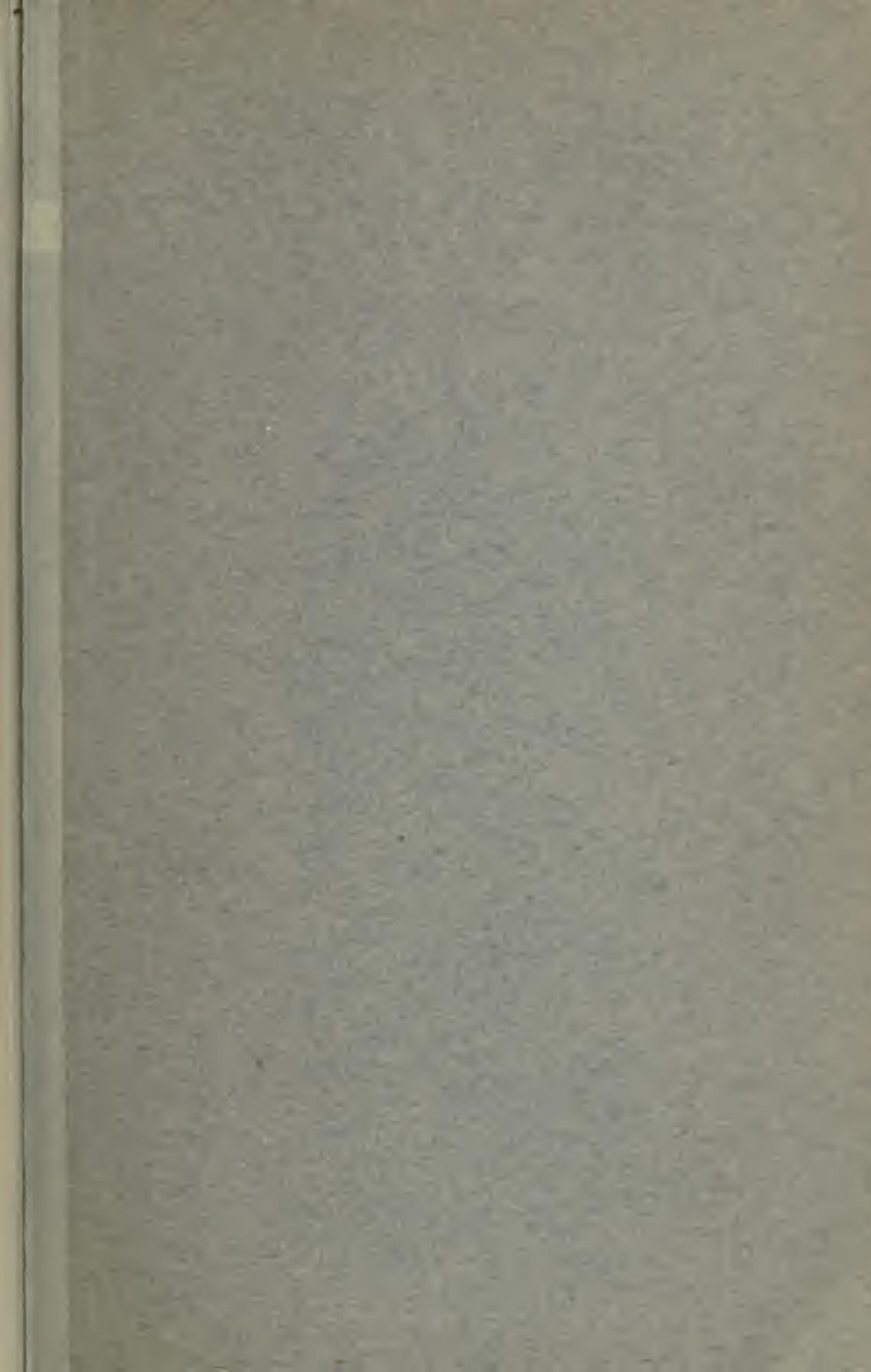


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