

Institution is no visible board of mataya off to yttromoep off, jasidua off to
eitl bus 1407 n i inhibits bus has doppes yd bawrot tng switnes
mewmum huba bus wooda shrub of vno hllqgs noitgoocoo. Institution
mataya is beavlni gulf bus ponepos lruig of bogusris omulov. Iupo. lo
omly n of bec

The Principles of Phyllotaxis.

BY

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

Lecturer in Natural Science, Jesus College, Oxford.

With seven Figures in the Text.

IN a preliminary note published some time ago¹, exception was taken to the conventional methods adopted for the description and even interpretation of phyllotaxis phenomena, and a suggestion was made that appeared to be not only more in accord with modern conceptions of the phenomena of energy distribution, but it was further indicated that such a theory when carried to its mathematical limits threw a strong light both on the mechanism of shoot production and the inherent mathematical properties of the lateral appendage usually described as a 'leaf-member,' as opposed to any secondary and subsidiary biological adaptations.

As publication of the entire paper has been delayed, and the new standpoint has not received any special support from botanists to whom the mathematical setting proved possibly a deterrent, the object of the present note is to place the entire argument of the original paper in as concise a form as possible². The preliminary discussion is sufficiently familiar³.

The conventional account of phyllotaxis phenomena involves a system of 'fractional expressions' which become interpreted into *angular divergences*; and in practice the appearance of 'orthostichies' has been taken as a guide to the determination of the proper 'fractional expression.' This method, elaborated by Schimper (1830-5), has more or less held the field to the present time; and, for want of something better, has received the assent, though often unwilling, of such great investigators as Hofmeister and Sachs, to say nothing of lesser lights. Although elaborated into a system by Schimper and Braun, who added the peculiar mathematical properties of the Fibonacci series to the academical account

¹ Note on Phyllotaxis, Annals of Botany, xv, p. 481, 1901.

² On the Relation of Phyllotaxis to Mechanical Laws. Part I, Construction by Orthogonal Trajectories, 1901. Part II, Asymmetry and Symmetry, 1902.

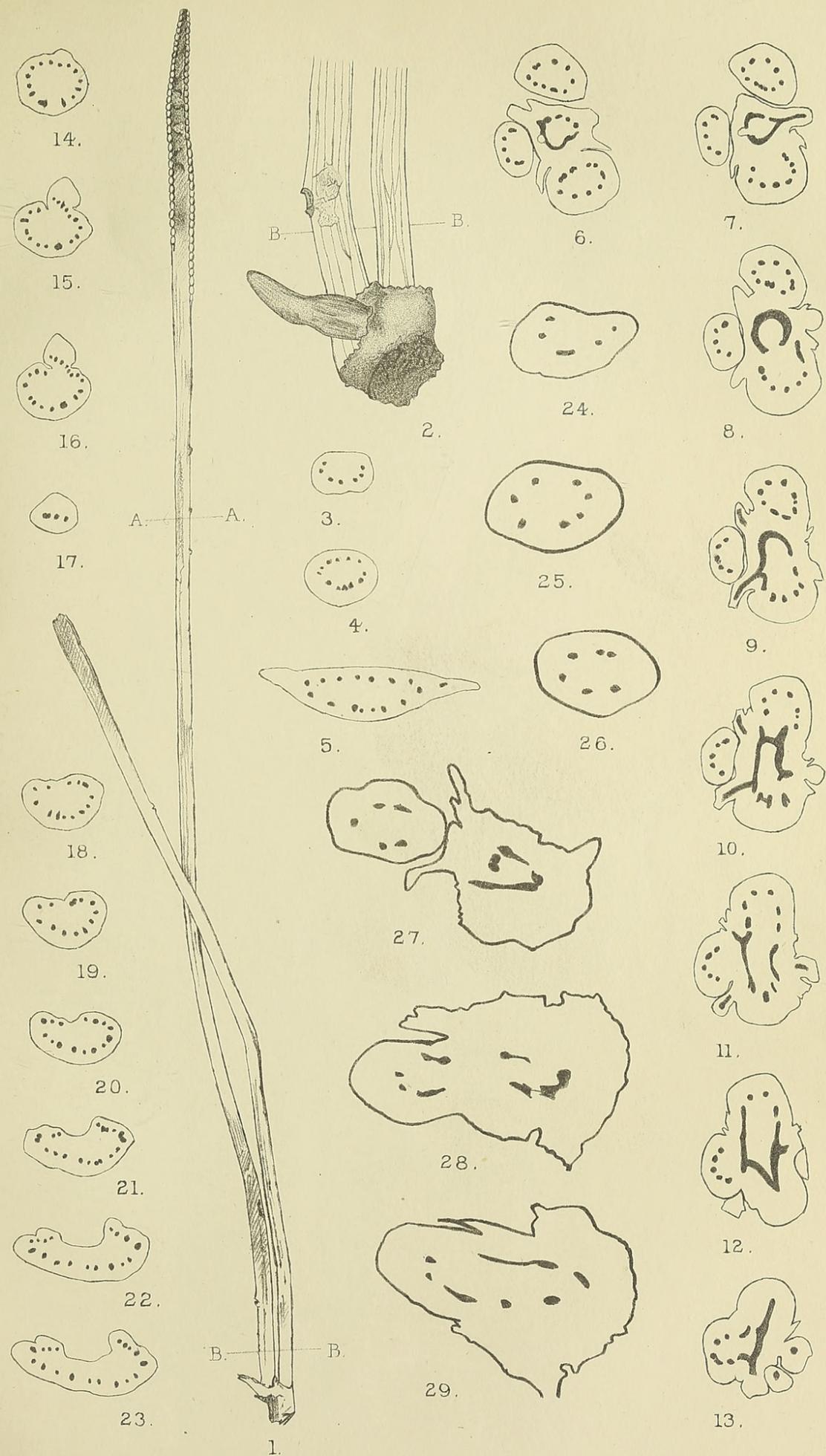
³ Descriptive Morphology-Phyllotaxis. New Phytologist, i, p. 49.

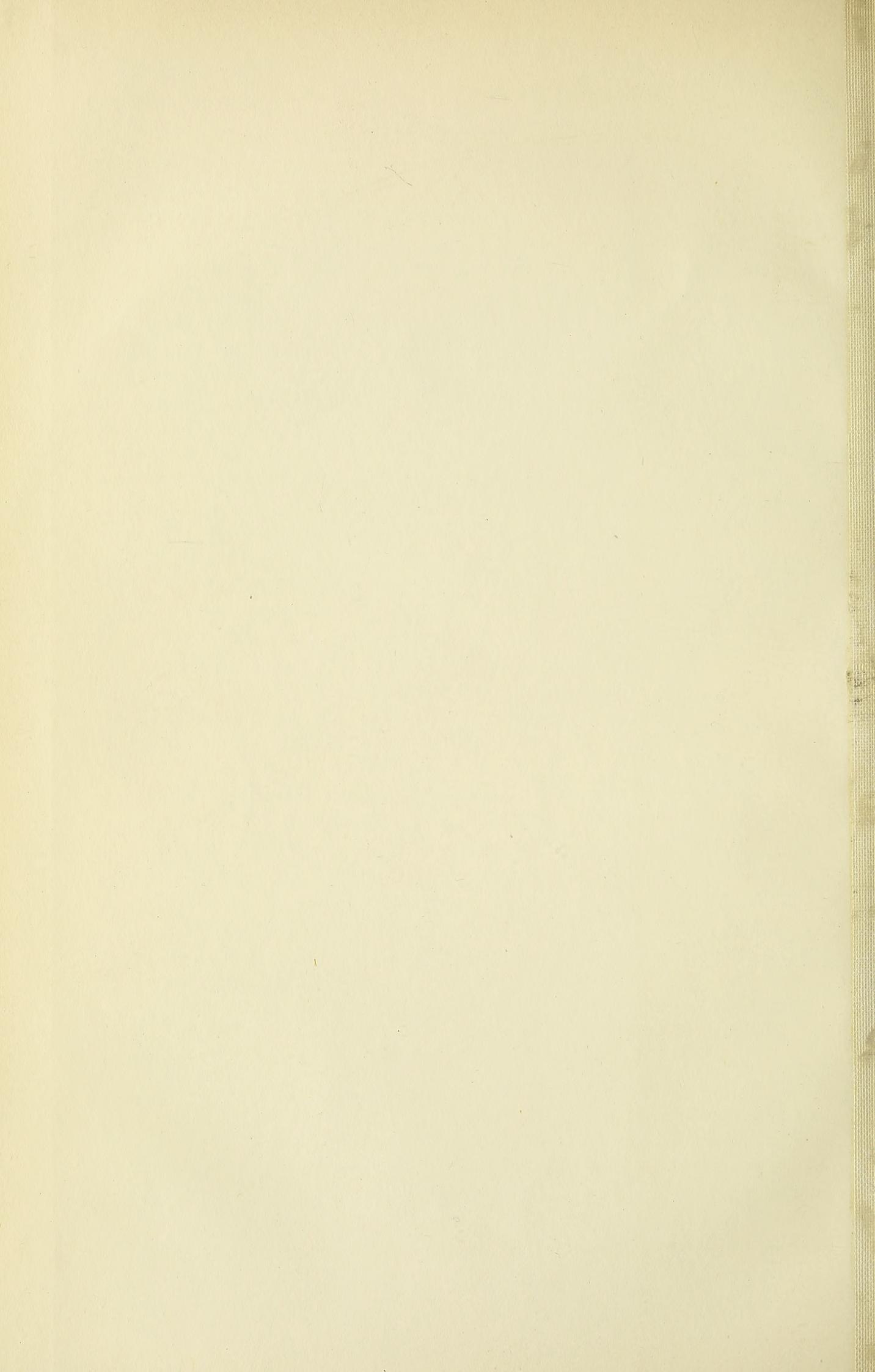
of the subject, the geometry of the system is based solely on a *mathematical conception* put forward by Bonnet and Calandrini in 1754; and this mathematical conception applied only to adult shoots and adult members of equal volume arranged in spiral sequence, and thus involved a system of *intersecting helices* of equal screw-thread, or, reduced to a plane expression, of spirals of Archimedes, also with equal screw-thread. A system of helical mathematics was thus interpolated into botanical science, and these helical systems were correctly tabulated by 'orthostichies' and 'divergence angles' obtained from simple fractional expressions themselves deduced from the observation of orthostichies.

But in transferring the study of phyllotaxis to the ontogenetic sequence of successively younger, and therefore *gradated*, primordia at the apex of a growing plant-shoot which was not cylindrical, these mathematical expressions were retained, although the helices originally postulated have absolutely vanished; and it is somewhat to the discredit of botanical science that this simple error should have remained so long undetected and unexpressed. As soon as one has to deal with spirals which have not an equal screw-thread, the postulated orthostichies vanish as straight lines; the fractional expressions therefore no longer present an accurate statement of the facts; and the divergence angles, calculated to minutes and seconds, are hopelessly out of the question altogether; while any contribution to the study of phyllotaxis phenomena which continues the use of such expressions must only serve to obscure rather than elucidate the interpretation of the phenomena observed. That the required orthostichies were really non-existent at the growing point, a feature well known to Bonnet himself, has thus formed the starting-point for new theories of *displacement* of hypothetically perfect helical systems, as, for example, in the contact-pressure theory of Schwendener. But once it is grasped that the practice of applying helical mathematics to spiral curves which, whatever they are, cannot be helices, is entirely beside the mark, it is clear that the sooner all these views and expressions are eliminated the better, and the subject requires to be approached without prejudice from an entirely new standpoint.

The first thing to settle therefore is what this new standpoint is to be; and how can such a remarkable series of phenomena be approached on any general physical or mathematical principles?

Now in a transverse section of a leaf-producing shoot, at the level of the growing point, the lateral appendages termed *leaves* are observed to arrange themselves in a gradated sequence as the expression of a *rhythmic production of similar protuberances*, which takes the form of a pattern in which the main construction lines appear as a grouping of intersecting curves winding to the centre of the field, which is occupied by the growing point of the shoot itself. As the mathematical properties





of such intersecting curve systems are not specially studied in an ordinary school curriculum, a preliminary sketch of some of their interesting features may be excused, since geometrical relationships have clearly no inherent connexion with the protoplasmic growth of the plant-shoot, but are merely properties of lines and numbers.

Thus, by taking first, for example, a system in which spiral curves of any nature radiate from a central point in such a manner that 5 are

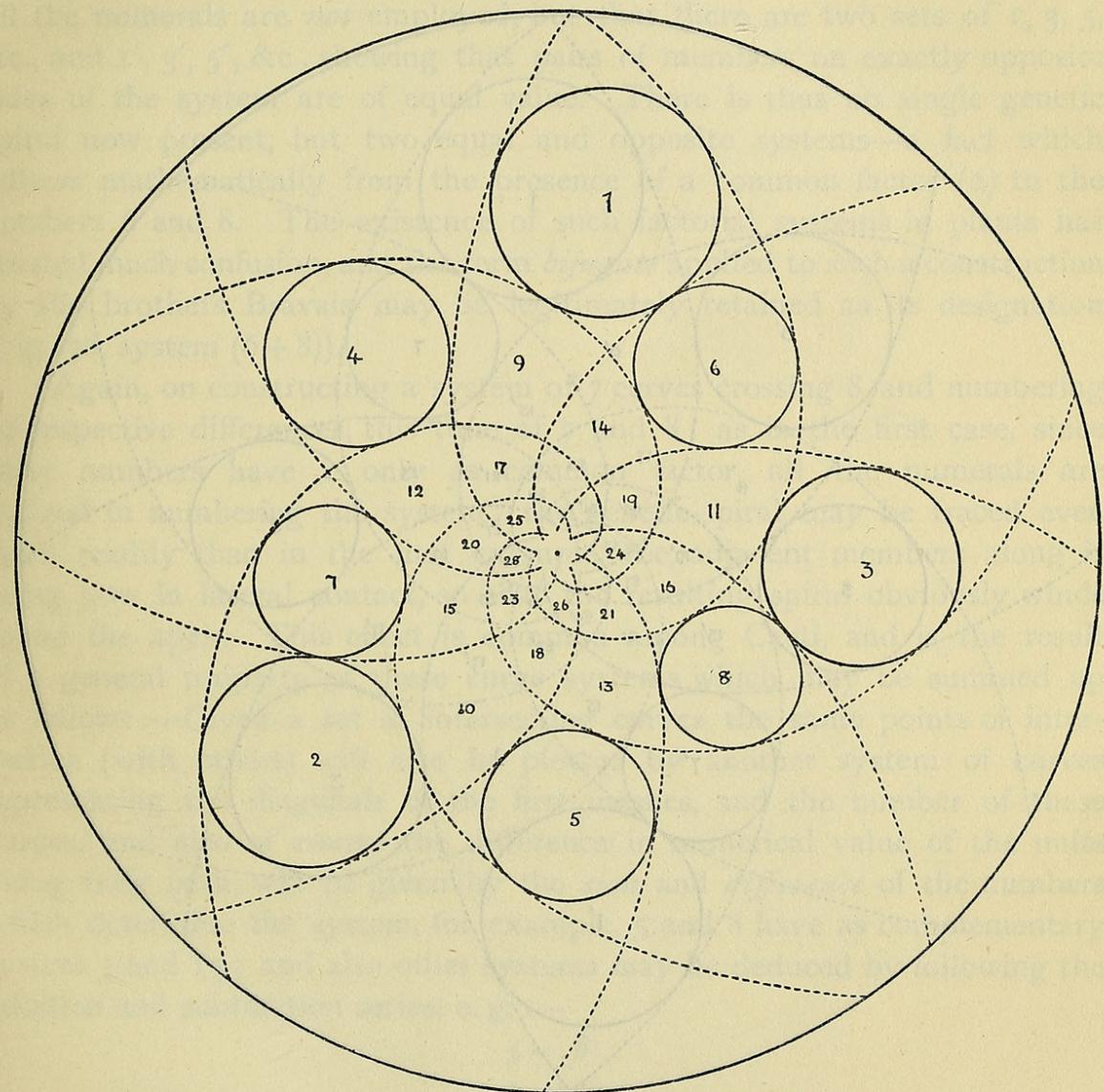


FIG. 35. Curve-system (5 + 8) : Fibonacci series. A full contact-cycle of eight members is represented by circular primordia.

turning in one direction and 8 in the other, giving points of intersection in a uniform sequence, a system of *meshes* and *points of intersection* is obtained, and to either of these units a numerical value may be attached. That is to say, if any member along the '5' curves be called 1, the next inmost member along the same series will be 6, since the whole system is made of 5 rows, and this series will be numbered by differences of 5.

In the same way differences of 8 along the '8' curves will give a numerical value to these members ; and by starting from 1, all the meshes, or points, if these are taken, may be numbered up as has been done in the figure (Fig. 35, (5 + 8)).

Observation of the figure now shows what is really a very remarkable property : all the numerals have been used, and 1, 2, 3, 4, &c., taken in order, give also a spiral sequence winding to the centre. This is merely

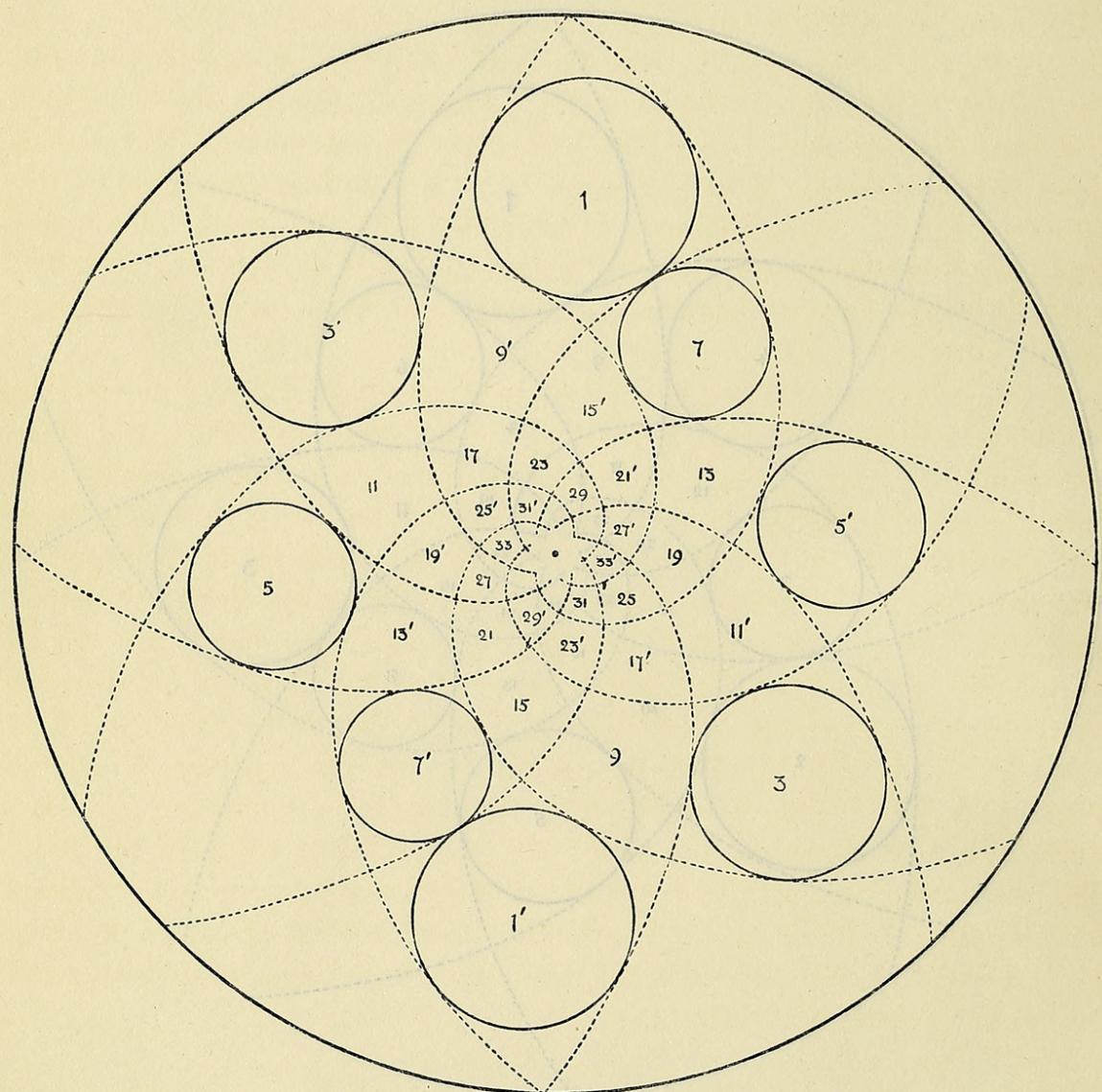


FIG. 36. Curve-system (6 + 8) : Bijugate type. Contact-cycle as in previous figure.

a mathematical property of the system (5 + 8), in that these numbers are only divisible by unity as a common factor ; but the single spiral thus obtained becomes in a botanical system the *genetic-spiral* which has been persistently regarded as the controlling factor in the whole system, since if such a construction be elongated sufficiently far, as on a plant-shoot, this spiral will alone be left visible.

The first point to be ascertained in phyllotaxis is the decision as to

which is to be the prime determining factor; that is to say, does the possession by the plant of a 'genetic-spiral' work out the subsidiary pattern of the parastichies, or are the parastichies the primary feature, and the genetic-spiral a secondary and unimportant consequence of the construction?

Now, other systems may quite as easily be drawn; thus take next a system of 6 curves crossing 8. On numbering these up by differences of 6 and 8 respectively in either series, it will be found that this time all the numerals are *not* employed, but that there are two sets of 1, 3, 5, &c., and 1', 3', 5', &c., showing that pairs of members on exactly opposite sides of the system are of equal value. There is thus no single genetic spiral now present, but two equal and opposite systems—a fact which follows mathematically from the presence of a common factor (2) to the numbers 6 and 8. The existence of such factorial systems in plants has created much confusion, and the term *bijugate* applied to such a construction by the brothers Bravais may be legitimately retained as its designation (Fig. 36, system (6 + 8)).

Again, on constructing a system of 7 curves crossing 8, and numbering by respective differences, this time of 7 and 8; as in the first case, since these numbers have 1 only as common factor, all the numerals are utilized in numbering the system; the genetic-spiral may be traced even more readily than in the first example, the adjacent members along it being now in lateral contact, so that the resulting spiral obviously winds round the apex. This effect is common among Cacti, and is the result of a general property of these curve systems which may be summed up as follows:—Given a set of intersecting curves, the same points of intersection (with others) will also be plotted by another system of curves representing the diagonals of the first meshes, and the number of these curves, and also of course the difference in numerical value of the units along their path, will be given by the *sum* and *difference* of the numbers which determine the system, for example, 5 and 8 have as complementary system 3 and 13; and also other systems may be deduced by following the addition and subtraction series, e. g. :—

$$5 - 8$$

$$3 - 13$$

$$2 - 21$$

$$1 - 34.$$

Whereas the (7 + 8) system gives only 1 and 15; the single so-called 'genetic-spiral,' which includes all the points, being reached at the first process. Thus a Cactus built on these principles would show an obvious 'genetic-spiral' winding on the apex and 15 ridges, which in the adult state become vertical as a true helical construction is secondarily produced as the internodes attain a uniform bulk (Fig. 37 (7 + 8)).

Finally, take the case of 8 curves crossing 8, and number in the same way by differences of 8 along both series. It immediately becomes clear that there are 8 similar series: all other spirals have been eliminated; there is no 'genetic-spiral' at all, but only a system of alternating circles of members of absolutely identical value in each circle. We have now, that is to say, systems of true *whorls*, and also learn in what a true whorl consists—the members must be exactly and

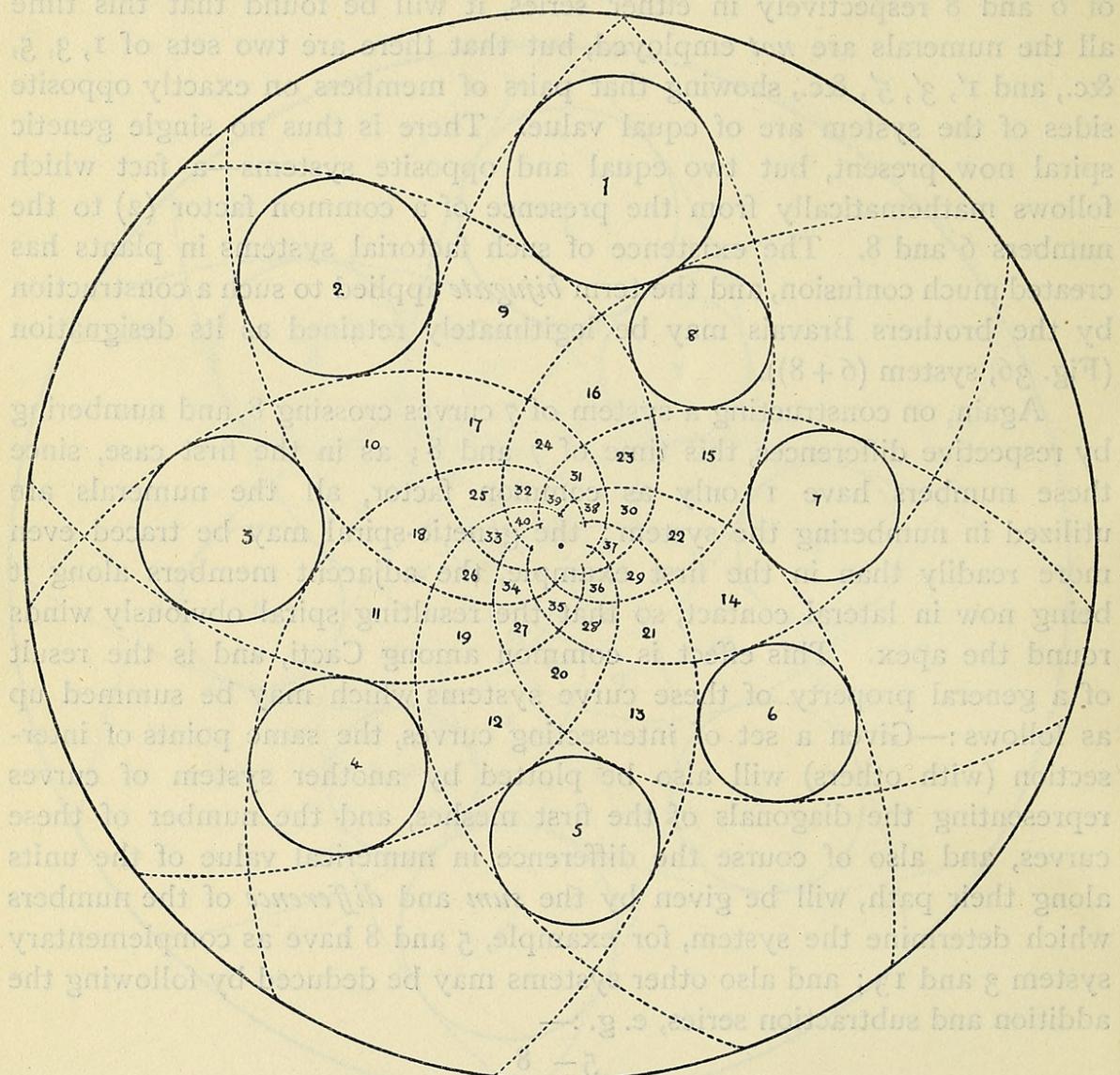


FIG. 37. Curve-system (7+8): anomalous type.

mathematically equal in origin—while the expression a *successive whorl* is a contradiction in terms.

From such simple and purely geometrical considerations it thus follows that the so-called 'genetic-spiral' is a property solely of intersecting curve-systems which only possess 1 as a common factor, and is therefore only existent in one case out of three possible mathematical forms (Figs. 35, 36, 38). While if these four systems were subjected to

a secondary *Zone of Elongation*, No. 1 would pull out as a complex of spirals in which four distinct sets might be traced; No. 2 as two spiral series leaving paired and opposite members at each 'node'; No. 3 as a spiral series with two complementary sets only; while No. 4 would give the familiar case of *alternating whorls* with 8 members at each 'node.' Further these cases are not merely arbitrary: they may all occur in the plant-kingdom, though the first is admittedly

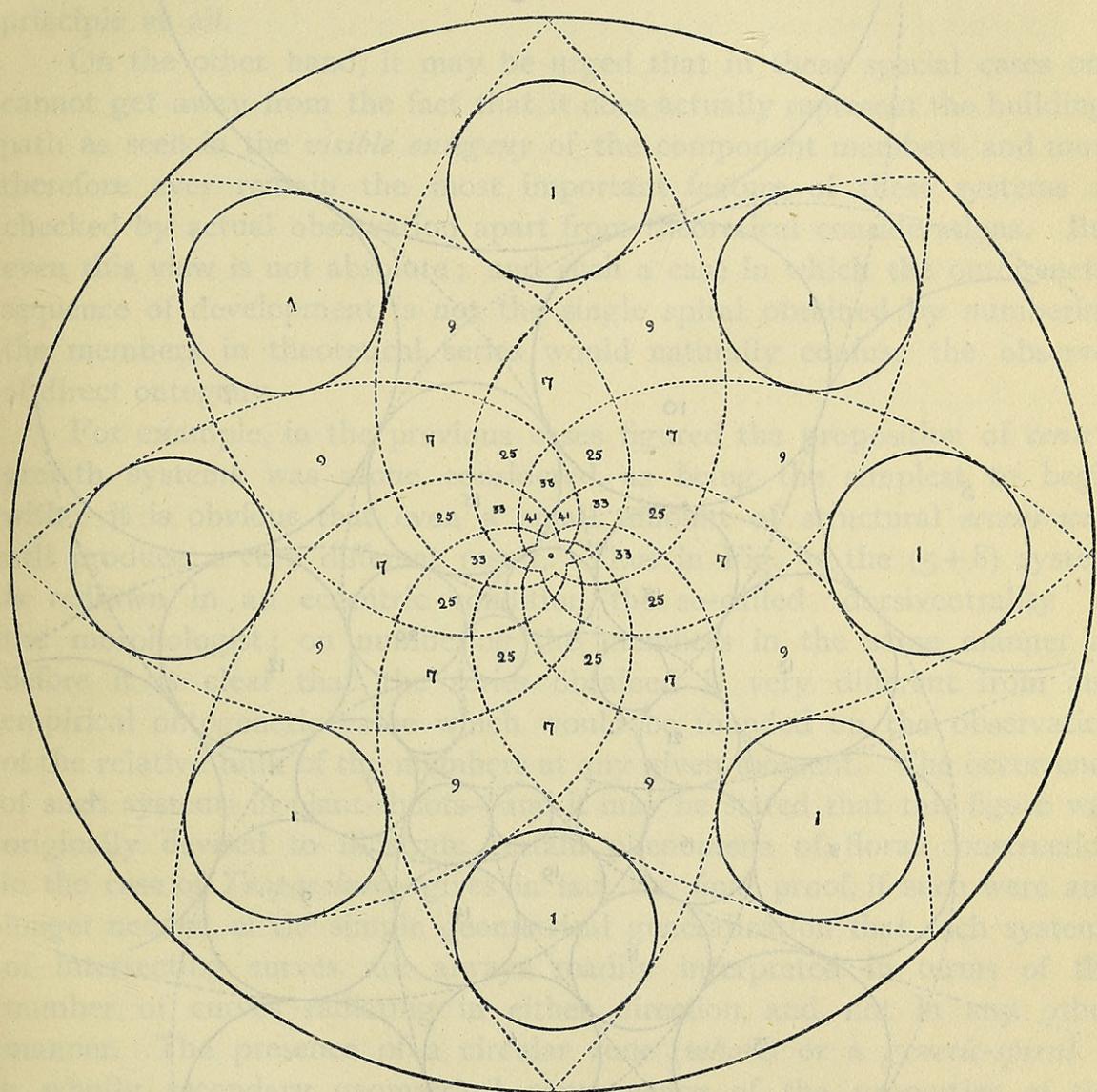


FIG. 38. Curve-system (8×8): symmetrical type.

the most frequent; but any theory which interprets one should equally well interpret the others. Similarly all changes of system may be discussed with equal readiness from the standpoint of the addition or loss of certain curves, and only from such a standpoint; since it is evident that once it is granted that new curves may be added to or lost from the system, the numerical relations of the members may be completely altered by

algunas de las que llamo "fibras" o "fibrales" que se observan en el sistema de la figura 39; basadas en el principio de que los óvalos que se forman en la construcción de la figura 39 son los óvalos que se forman en la construcción de la figura 38, pero con un factor de multiplicación de 5 en vez de 3.

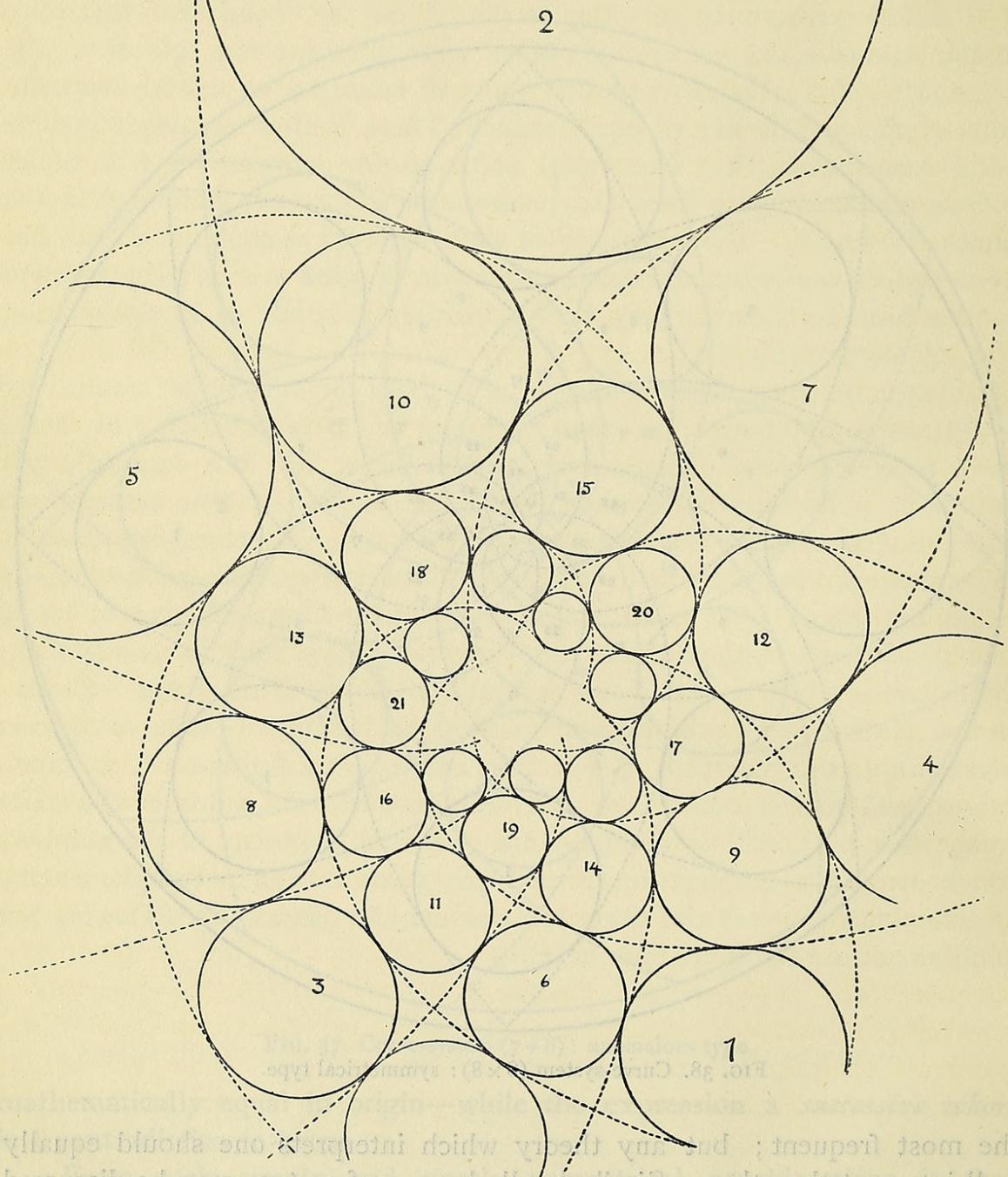


FIG. 39. System (5+8): eccentric construction in the plane of No. 2. Is upo este sistema que se forman los óvalos que se observan en la figura 39; basados en el principio de que los óvalos que se forman en la construcción de la figura 39 son los óvalos que se forman en la construcción de la figura 38, pero con un factor de multiplicación de 5 en vez de 3.

the addition of one curve only, as in the difference between the systems $(7+8)$, $(8+8)$, &c. (Figs. 35–38)¹.

Thus the hypothesis of a *genetic-spiral*, since it entirely fails to account for the arrangement of the members of all phyllotaxis systems in a single spiral, may be conveniently wholly eliminated from future discussions of these systems. It remains as a mere geometrical accident of certain intersecting curve-systems, and the fact that such systems may be very common in plant construction does not affect the main principle at all.

On the other hand, it may be urged that in these special cases one cannot get away from the fact that it does actually represent the building-path as seen in the *visible ontogeny* of the component members, and must therefore ever remain the most important feature of these systems as checked by actual observation apart from theoretical considerations. But even this view is not absolute; and such a case in which the ontogenetic sequence of development is not the single spiral obtained by numbering the members in theoretical series would naturally confuse the observer of direct ontogeny.

For example, in the previous cases figured the proposition of *centric* growth systems was alone considered, as being the simplest to begin with; it is obvious that even a small amount of structural *eccentricity* will produce a very different result. Thus in Fig. 39 the $(5+8)$ system is redrawn in an eccentric condition, the so-called ‘dorsiventrality’ of the morphologist; on numbering the members in the same manner as before it is clear that the series obtained is very different from any empirical ontogenetic value which would be founded on the observation of the relative bulk of the members at any given moment. The occurrence of such systems in plant-shoots—and it may be stated that this figure was originally devised to illustrate certain phenomena of floral construction in the case of *Tropaeolum*—gives in fact the final proof, if such were any longer needed, of the simple geometrical generalization that such systems of intersecting curves are always readily interpreted in terms of the number of curves radiating in either direction, and not in any other manner. The presence of a circular zone (*whorl*) or a *genetic-spiral* is a wholly secondary geometrical consequence of the properties of the numerals concerned in constructing the system. The preference of any individual botanist, either in the past or at present, for any particular method

¹ Cf. Relation of Phyllotaxis to Mechanical Laws. Part II, p. 109, Rising and Falling Phyllotaxis. Part IV, Cactaceae.

Though the figures (35–38) have, as a matter of fact, been drawn by means of suitable orthogonally intersecting logarithmic spirals, because these curves are easily obtained and the schemes are subsequently held to be the representation of the true construction system of the plant-apex, the nature of the spirals does not affect the general laws of intersection so long as this takes place uniformly.

of interpreting any of these systems has little bearing on the case: the subject is purely a mathematical one; and the only view which can be acceptable is that which applies equally well to all cases, in that the question is solely one of the geometrical properties of lines and numbers, and must therefore be settled without reference to the occurrence of such constructions in the plant.

If all phyllotaxis systems are thus to be regarded solely as cases of intersecting curves, which are selected in varying numbers in the shoots of different plants, and often in different shoots of the same plant, with a tendency to a specific constancy which is one of the marvellous features of the plant-kingdom, it remains now to discuss the possibility of attaching a more direct significance to these curves, which in phyllotaxis construction follow the lines of what have been termed the *contact-parastichies*; that is to say, to consider

- I. What is the mathematical nature of the spirals thus traced?
- II. What is the nature of the intersection?
- III. Is it possible to find any analogous construction in the domain of purely physical science?

The suggestion of the logarithmic spiral theory is so obvious that it would occur naturally to any physicist: the spirals are primarily of the nature of *logarithmic spirals*; the intersections are *orthogonal*; and the construction is directly analogous to the representation of lines of equipotential in a simple plane case of electrical conduction. In opposition to this most fruitful suggestion, it must be pointed out however that the curves traced on a section are obviously never logarithmic spirals, and the intersections cannot be measured as orthogonal. But then it is again possible that in the very elaborate growth-phenomena of a plant-shoot secondary factors come into play which tend to obliterate the primary construction; in fact, in dealing with the great variety of secondary factors, which it only becomes possible to isolate when the primary construction is known, the marvel is rather that certain plants should yield such wonderfully approximately accurate systems. To begin with, logarithmic spiral constructions are *infinite*, the curves pass out to infinity, and would wind an infinite number of times before reaching the pole. Plant constructions on the other hand are *finite*, the shoot attains a certain size only, and the pole is relatively large. The fact that similar difficulties lie in the application of strict mathematical construction to a vortex in water, for example, which must always possess an axial tube of flow for a by no means perfect fluid, or to the distribution of potential around a wire of appreciable size, does not affect the essential value of the mathematical conception to physicists. And, though the growth of the plant is finite, and therefore necessarily subject to retarding influences of some kind, there is no reason why a region may not be postulated,

however small, at which such a mathematical distribution of 'growth-potential' may be considered as accurate; and such a region is here termed a '*Growth-Centre*.' Since the interpretation of all complex phenomena must be first attacked from the standpoint of simple postulates, it now remains to consider the construction and properties of as simple a centre of growth as possible.

Thus in the simplest terms the growth may be taken as *uniform*

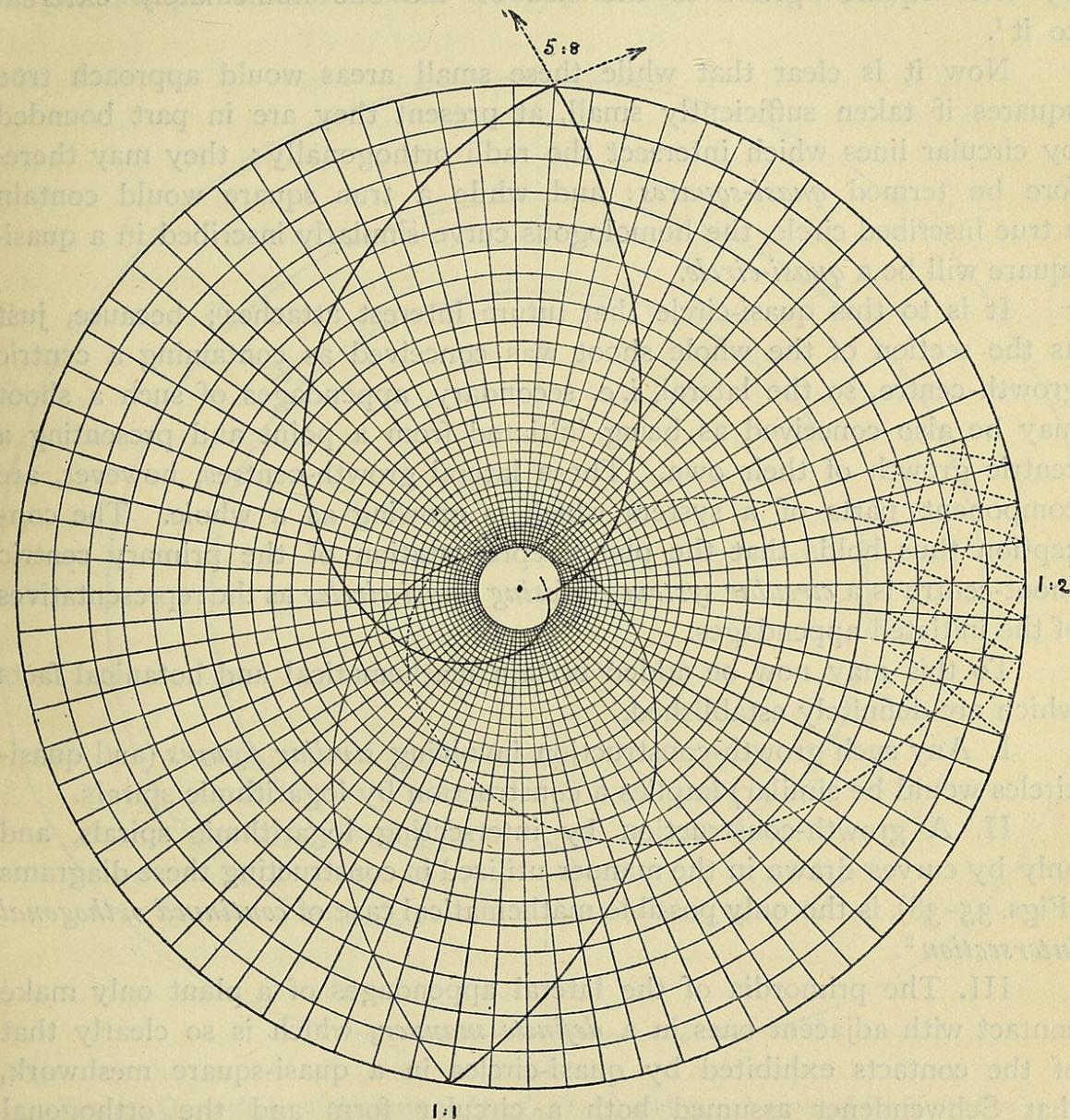


FIG. 40. Scheme for Uniform Growth Expansion: a circular meshwork of quasi-squares. Symmetrical construction from which asymmetrical homologues are obtained by the use of logarithmic spirals.

and *centric*: the fact that all plant growth is subject to a *retardation* effect or may be frequently *eccentric*, may at present be placed wholly on one side, since the simplest cases evidently underlie these. The case of uniform centric growth is that of a uniformly expanding sphere; or,

since it is more convenient to trace a solid in separate planes, it will be illustrated by a diagram in which a system of concentric circles encloses a series of similar figures, which represent a uniform growth increment in equal intervals of time. Such a circular figure, in which the expanding system is subdivided into an indefinite number of small squares representing equal time-units, is shown in Fig. 40, and presents the general theory of mathematical growth, in that in equal times the area represented by one 'square' grows to the size of the one immediately external to it¹.

Now it is clear that while these small areas would approach true squares if taken sufficiently small, at present they are in part bounded by circular lines which intersect the radii orthogonally; they may therefore be termed *quasi-squares*: and while a true square would contain a true inscribed circle, the homologous curve similarly inscribed in a quasi-square will be a *quasi-circle*.

It is to this quasi-circle that future interest attaches; because, just as the section of the whole shoot was conceived as containing a centric growth-centre, so the lateral, i. e. secondary, appendages of such a shoot may be also conceived as being initiated from a point and presenting a centric growth of their own. These lateral growth-centres, however, are component parts of a system which is growing as a whole. The conception thus holds that the plane representation of the primary centric shoot-centre is a *circular system enclosing quasi-circles* as the representatives of the initiated appendages.

To this may now be added certain mathematical and botanical facts which are definitely established.

I. Any such growth-construction involving *similar figures* (and quasi-circles would be similar) implies a construction by logarithmic spirals.

II. A growth-construction by intersecting logarithmic spirals, and only by curves drawn in the manner utilized in constructing these diagrams (Figs. 35–38), is the only possible mathematical case of *continued orthogonal intersection*².

III. The primordia of the lateral appendages of a plant only make contact with adjacent ones in a *definite manner*, which is so clearly that of the contacts exhibited by quasi-circles in a quasi-square meshwork, that Schwendener assumed both a circular form and the orthogonal arrangement as the basis of his Dachstuhl Theory: these two points being here just the factors for which a rigid proof is required, since given these the logarithmic spiral theory necessarily follows.

A construction in terms of quasi-circles would thus satisfy all theo-

¹ The same figure may also be used to illustrate a simple geometrical method of drawing any required pair of orthogonally intersecting logarithmic spirals.

² For the formal proof of this statement I am indebted to Mr. H. Hilton.

retical generalizations of the mathematical conception of uniform growth, and would be at the same time in closest agreement with the facts of observation; while no other mathematical scheme could be drawn which would include primordia arranged in such contact relations and at the same time give an orthogonal construction. If, that is to say, the *quasi-circle* can be established as the mathematical representative of the primordium of a lateral appendage, the orthogonal construction, which is the one point most desired to be proved, will necessarily follow.

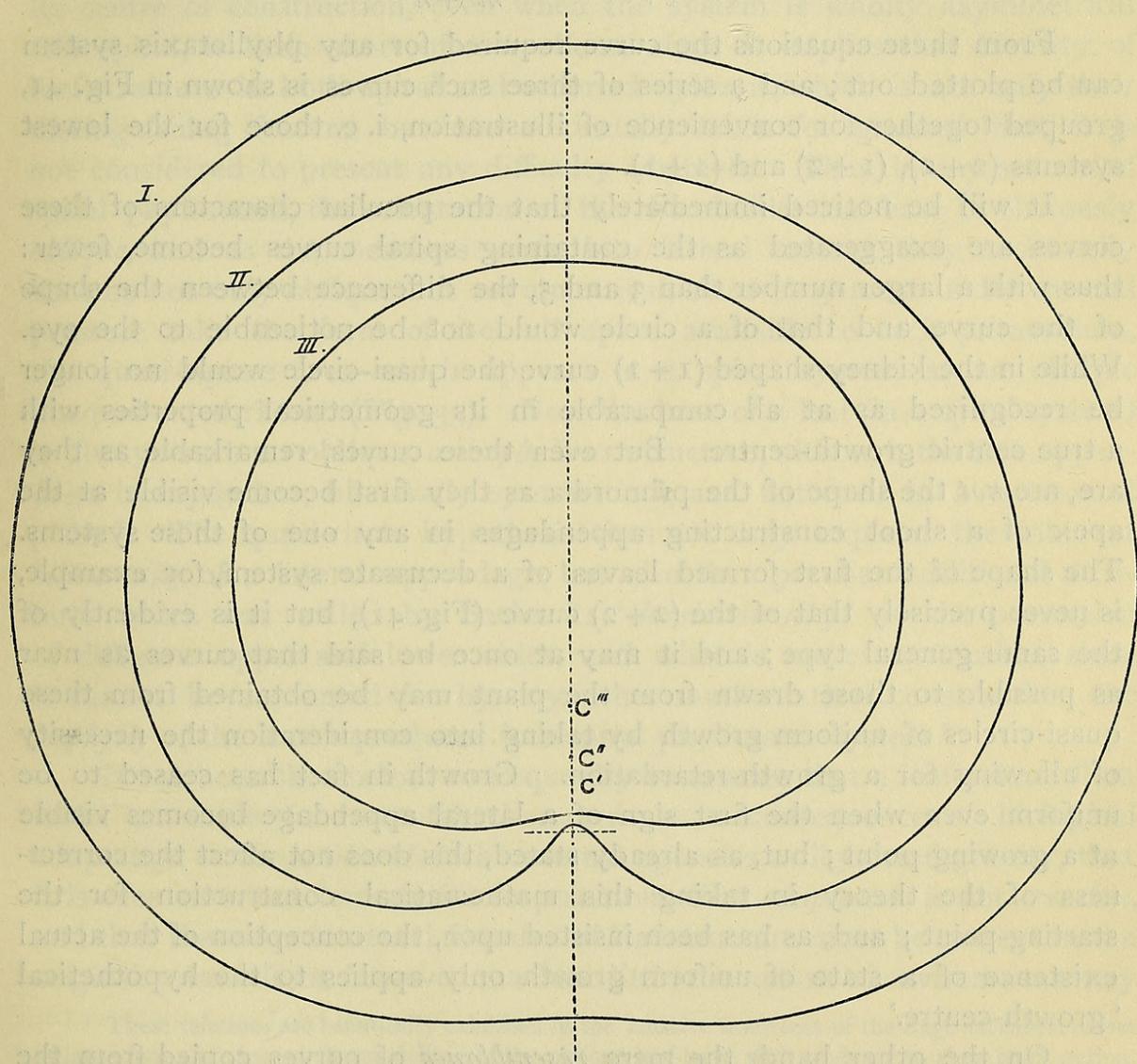


FIG. 41. Quasi-circles of the systems $(2+2)$, $(1+1)$ and $(1+2)$ arranged for illustration in the plane of median symmetry. C' , C'' , C''' , the centres of construction of the respective curves. (After E. H. Hayes.)

It remains therefore now to discuss the nature of the curves denoted by the term *quasi-circles*; their equations may be deduced mathematically, and the curves plotted on paper from the equations. These determinations have been made by Mr. E. H. Hayes. Thus a general equation for the quasi-circular curve inscribed in a mesh made by the orthogonal inter-

section of m spirals crossing n , in the manner required, is given in such a form as,

$$\log r = \log c \pm 1.36438 \sqrt{\frac{1}{m^2 + n^2} - .000030864 \theta^2},$$

where the logarithm is the tabular logarithm, and θ is measured in degrees; or where the logarithm is the natural logarithm and θ in circular measure:

$$\left(\log \frac{r}{c}\right)^2 + \theta^2 = \frac{\pi^2}{m^2 + n^2}.$$

From these equations the curve required for any phyllotaxis system can be plotted out; and a series of three such curves is shown in Fig. 41, grouped together for convenience of illustration, i. e. those for the lowest systems ($2+2$), ($1+2$) and ($1+1$).

It will be noticed immediately that the peculiar characters of these curves are exaggerated as the containing spiral curves become fewer: thus with a larger number than 3 and 5, the difference between the shape of the curve and that of a circle would not be noticeable to the eye. While in the kidney-shaped ($1+1$) curve the quasi-circle would no longer be recognized as at all comparable in its geometrical properties with a true centric growth-centre. But even these curves, remarkable as they are, are *not* the shape of the primordia as they first become visible at the apex of a shoot constructing appendages in any one of these systems. The shape of the first formed leaves of a decussate system, for example, is never precisely that of the ($2+2$) curve (Fig. 41), but it is evidently of the same general type; and it may at once be said that curves as near as possible to those drawn from the plant may be obtained from these quasi-circles of uniform growth by taking into consideration the necessity of allowing for a growth-retardation. Growth in fact has ceased to be uniform even when the first sign of a lateral appendage becomes visible at a growing point; but, as already stated, this does not affect the correctness of the theory in taking this mathematical construction for the starting-point; and, as has been insisted upon, the conception of the actual existence of a state of uniform growth only applies to the hypothetical 'growth-centre.'

On the other hand, the mere *resemblance* of curves copied from the plant to others plotted geometrically according to a definite plan which is however modified to fit the facts of observation, will afford no strict proof of the validity of the hypothesis, although it may add to its general probability, since there is obviously no criterion possible as to the actual nature of the growth-retardation; that is to say, whether it may be taken as uniform, or whether, as may be argued from analogy, it may exhibit daily or even hourly variations. Something more than this is necessary before the correctness of the assumption of quasi-circular leaf-homologues can

be taken as established; and attention may now be drawn to another feature of the mathematical proposition.

It follows from the form of the equation ascribed to the quasi-circle that whatever value be given to m and n , the curve itself is *bilaterally symmetrical* about a radius of the whole system drawn through its centre of construction. That it should be so when $m=n$, i.e. in a symmetrical (*whorled*) leaf-arrangement, would excite no surprise; but that the primordium should be bilaterally symmetrical about a radius drawn through its centre of construction, even when the system is wholly asymmetrical and spiral, is little short of marvellous, since it implies that identity of leaf-structure in both spiral and whorled systems, which is not only their distinguishing feature, but one so usually taken for granted that it is not considered to present any difficulty whatever. Thus, in any system of spiral phyllotaxis, the orientation of the rhomboidal leaf-base is obviously *oblique*, and as the members come into lateral contact they necessarily become not only oblique but *asymmetrical*, since they must under mutual pressure take the form of the full space available to each primordium, the quasi-square area which appears in a spiral system as an oblique unequal-sided rhomb (Fig. 35). Now the base of a leaf (in a spiral system) is always such an oblique, *anisophyllum* structure, although the free appendage is *isophyllum*, bilaterally symmetrical, and flattened in a horizontal plane¹. The quasi-circle hypothesis thus not only explains the inherent *bilaterality* of a lateral appendage, but also that peculiar additional attribute which was called by Sachs its '*dorsiventrality*,' or the possession of different upper and lower sides, and what is more remarkable, since it cannot be accounted for by any other mathematical construction, the *isophylly* of the leaves produced in a spiral phyllotaxis system².

It has been the custom so frequently to assume that a leaf-primordium takes on these fundamental characters as a consequence of biological adaptation to the action of such external agencies as light and gravity, that it is even now not immaterial to point out that *adaptation* is not *creation*, and that these fundamental features of leaf-structure must be present in the original primordium, however much or little the action of environment may

¹ These relations are beautifully exhibited in the massive insertions of the huge succulent leaves of large forms of *Agave*: the modelling of the oblique leaf-bases with tendency to rhomboid section, as opposed to that of the horizontal symmetrical portion of the upper free region of the appendage, may be followed by the hand, yet only differs in bulk from the case of the leaves of *Sempervivum* or the still smaller case of the bud of *Pinus*.

² *Anisophylly* is equally a mathematical necessity of all *eccentric* shoot systems.

It will also be noted that the *adjustment* required in the growing bud, as the free portions of such spirally placed primordia tend to orientate their bilaterally symmetrical lamina in a radial and not spiral plane, gives the clue to those peculiar movements in the case of spiral growth systems, which, in that they could be with difficulty accounted for, although as facts of observation perfectly obvious, has resulted in the partial acceptance of Schwendener's Dachstuhl Theory. This theory was in fact mainly based on the necessity for explaining this 'slipping' of the members, but in the logarithmic spiral theory it follows as a mathematical property of the construction.

result in their becoming obvious to the eye. The fact that the quasi-circle hypothesis satisfies all the demands of centric growth systems, whether symmetrical or asymmetrical, as exhibited in the fundamental character of foliar appendages, and that these characters may be deduced as the mathematical consequences of the simple and straightforward hypothesis of placing centres of lateral growth in a centric system which is also growing, may be taken as a satisfactory proof of the correctness of the original standpoint. And it is difficult to see what further proof of the relation between a leaf-primordium as it is first initiated, and the geometrical properties of a quasi-circle growth system is required ; but it still remains to connect this conception with that of orthogonal construction.

This however naturally follows when it is borne in mind, firstly that no other asymmetrical mathematical growth-construction is possible, except the special quasi-square system which will include such quasi-circles ; and secondly, that the contact-relations of the quasi-circles in these figures are identical with those presented by the primordia in the plant, and could only be so in orthogonal constructions. It thus follows that with the proving of the quasi-circle hypothesis, the proof is further obtained that the intersection of the spiral paths must be mutually orthogonal ; and it becomes finally established that in the construction of a centric phyllotaxis system, along logarithmic spiral lines, the segmentation of the growth system at the hypothetical growth-centre does follow the course of paths intersecting at right angles ; and the principle of construction by orthogonal trajectories, originally suggested by Sachs for the lines of cell-structure and details of thickened walls, but never more fully proved, is now definitely established for another special case of plant-segmentation, which involves the production of lateral appendages without any reference to the segmentation of the body into 'cell' units.

But even this is not all ; the point still remains,—What does such construction imply in physical terms ? Nor can it be maintained that the present position of physical science affords any special clue to the still deeper meaning of the phenomena. The fact that the symmetrical construction in terms of logarithmic spirals agrees with the diagram for distribution of lines of equipotential and paths of current flow in a special case of electric conduction, while the asymmetrical systems are similarly homologous with lines of equal pressure and paths of flow in a vortex in a perfect fluid, the former a static proposition, the latter a kinetic one, may be only an 'accident.' On the other hand it must always strike an unprejudiced observer that there may be underlying all these cases the working of some still more fundamental law which finds expression in a similar mathematical form.

In conclusion, it may be noted that if the proof here given of the principle of plant construction by orthogonal trajectories is considered satis-

factory, it adds considerably to the completeness of the principles of protoplasmic segmentation, and may be extended in several directions with further interesting results. It is only necessary to point out that the case of centric-growth is after all only a first step; and the most elaborate growth forms of the plant-kingdom, as exhibited for instance in the segmentation of the leaf-lamina, may be approached along similar lines, and by means of geometrical constructions which are consequent on the more or less perfect substitution of *eccentric* and ultimately wholly *unilateral* growth-extension, which again must ever be of a retarded type. The subject thus rapidly gains in complexity; but that the study of growth-form, which after all is the basis of all morphology, must be primarily founded on such simple conceptions as that of the 'growth-centre' which has here been put forward, should I think receive general assent, and in the case of the quasi-circle, there can be little doubt as to the extreme beauty of the results of the mathematical consideration.



Church, A. H. 1904. "The principles of phyllotaxis." *Annals of botany* 18, 227–243. <https://doi.org/10.1093/oxfordjournals.aob.a088960>.

View This Item Online: <https://www.biodiversitylibrary.org/item/234469>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a088960>

Permalink: <https://www.biodiversitylibrary.org/partpdf/318757>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.