On the Relation of Phyllotaxis to Mechanical Laws

On the
Relation of Phyllotaxis
to Mechanical Laws

By

Arthur Harry Church, M.A., D.Sc.

Lecturer in Natural Science, Jesus College, Oxford

Contents

PART I.

CONSTRUCTION BY ORTHOGONAL TRAJECTORIES.

PART II.

ASYMMETRICAL AND SYMMETRICAL PHYLLOTAXIS.

v

PART III.

SECONDARY GROWTH-PHENOMENA.

MATHEMATICAL NOTES ON LOG: SPIRAL SYSTEMS AND
THEIR APPLICATION TO PHYLLOTAXIS PHENOMENA.

Note on Phyllotaxis.

BY

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

Lecturer in Natural Science, Jesus College, Oxford.

—••—

With two Figures in the Text.

—••—

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

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

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

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

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

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

    1. The assumption of a special divergence-angle.

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

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

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

Such investigation shows that the hypotheses have no true basis, while the construction by spirals of Archimedes is a conspicuous failure. Thus, the divergence-angle is hope-lessly beyond the error of actual observation on the plant, since the points from which the angles have to be taken must be judged by the eye ; when, therefore, the divergence-angles are expected to be true to a matter of minutes and seconds in fairly high divergences, this becomes a matter of impossibility ; and the Bravais showed in 1835 that it was in fact impossible to *disprove* the standpoint that there was only one angular divergence in such cases of normal Fibonacci phyllotaxis, namely Schimper's 'Ideal Angle' of 137°, 30′, 27″·936. Similarly, it is equally impossible to judge straight lines by the eye alone, and the existence of *orthostichies* in spiral phyllotaxis as mathematically straight lines thus becomes as hypothetical as the Schimper-Braun divergence-angles. In neither of the two methods used for the practical deter-mination of phyllotaxis-constants is there then any possibility of accurate mathematical demonstration. Although the tabulation of appearances as judged by the eye may be taken as an approximately accurate version of the real

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

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

Thus, from the equation to the Archimedean spiral ($r = a\theta$), it is easy to construct a pair of spirals whose variable a shall have the ratio of the parastichies observed on any given specimen. Take for example the $\frac{8}{21}$ system, the primary contact parastichies of which are 8 and 13 ; Fig. 2 shows such a system geometrically planned for a left-hand genetic spiral: the members along the twenty-one orthostichy lines differ by twenty-one, and fall on the mathematically straight radii vectores of the system. The intersections of these parastichy spirals mark the *points* at which the lateral members are inserted, and the views of Schimper and Braun included only the consideration of such points. It is clear, however, that if the spaces between the spiral planes are regarded as containing the members pressed into close lateral contact, as seen in the transverse section of a foliage bud, the appearance of the progressive dorsiventrality of such lateral members is very fairly *imitated*. The construction, in fact, becomes more and more like the appearances seen in the plant as the periphery of the system is reached, but the central part which includes the actual seat of development is very inadequately represented: thus, the areas become so relatively elongated in the

radial direction as they approach the centre that they cannot possibly represent any formation of primordia at the stem-apex, on which such members are well known to arise as fairly isodiametric protuberances.   At the same time, it will be noticed that the Archimedean spirals by construction all fall into the centre and stop there, so that no room is left in the
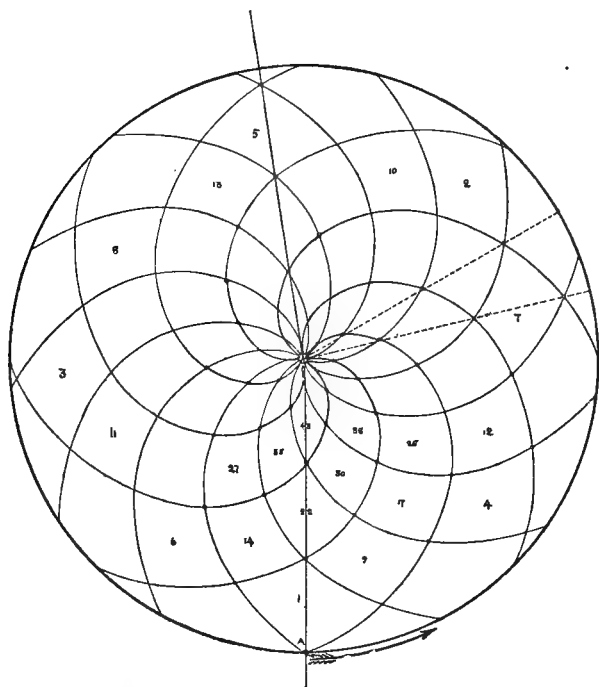
Fig. 2. Theory of Schimper and Braun.   Construction for Phyllotaxis $\frac{8}{21}$.
$OA.$ = Orthostichy line = radius vector passing through 1, 22, 43, &c.   Members along the contact parastichies differ by 8 and 13 respectively.   Genetic spiral winds left.   Divergence-angle = $\frac{8}{21}$ of $360° = 137° \ 8' \ 34''$.

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

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

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

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

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

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

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

construction gives the true key to the problem, and that the
whole subject thus becomes a question of the mechanical dis-
tribution of energy within the substance of the protoplasmic
mass of the plant-apex : that phyllotaxis phenomena are the
result of inherent properties of protoplasm, the energy of life
being in fact distributed according to the laws which govern
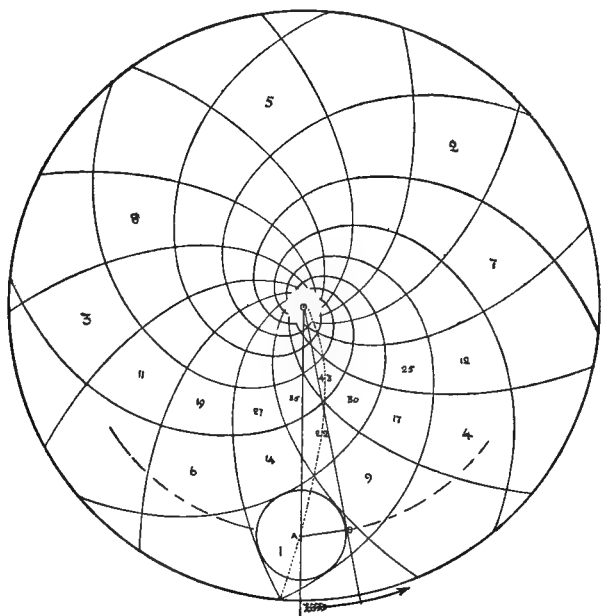
Fig. 3. Log. spiral theory : Construction for Phyllotaxis system (8 + 13) in
terms of distribution of energy.   Contact Parastichies = orthogonally intersecting
log. spirals in ratio (8 : 13).   The curve through 1, 22, 43, &c., is also a log. spiral.
Genetic spiral winds left.   Divergence-angle = 137° 30′ 38″. *Bulk-ratio* of axis
to primordium = OA., $AB.$ = 1 : 5 within a small error, or = Sin AOB = ·204 for
the true curve.

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

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

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

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

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

On the other hand it will be noted that the new constructions are equally incapable of absolute verification by any angular measurements on the plant; Schimper's orthostichies have vanished, as pointed out by the Bravais, for the more general examples of phyllotaxis, and the difference between the two spiral systems is very slight to the eye: but, while the Schimper-Braun School only sought to imitate the appearances seen on the plant, the log. spiral theory gives at least an equally correct summary of the facts observed, and is in addition founded on definite mechanical laws of construction by orthogonal trajectories which have already been accepted for plant anatomy; it is so far then the logical outcome of Sachs' theory of the orthogonal intersection of cell-walls, and represents therefore another special case of the distribution of energy along planes of equal action [1].

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

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 ago[1], 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 possible[2]. The preliminary discussion is sufficiently familiar[3].

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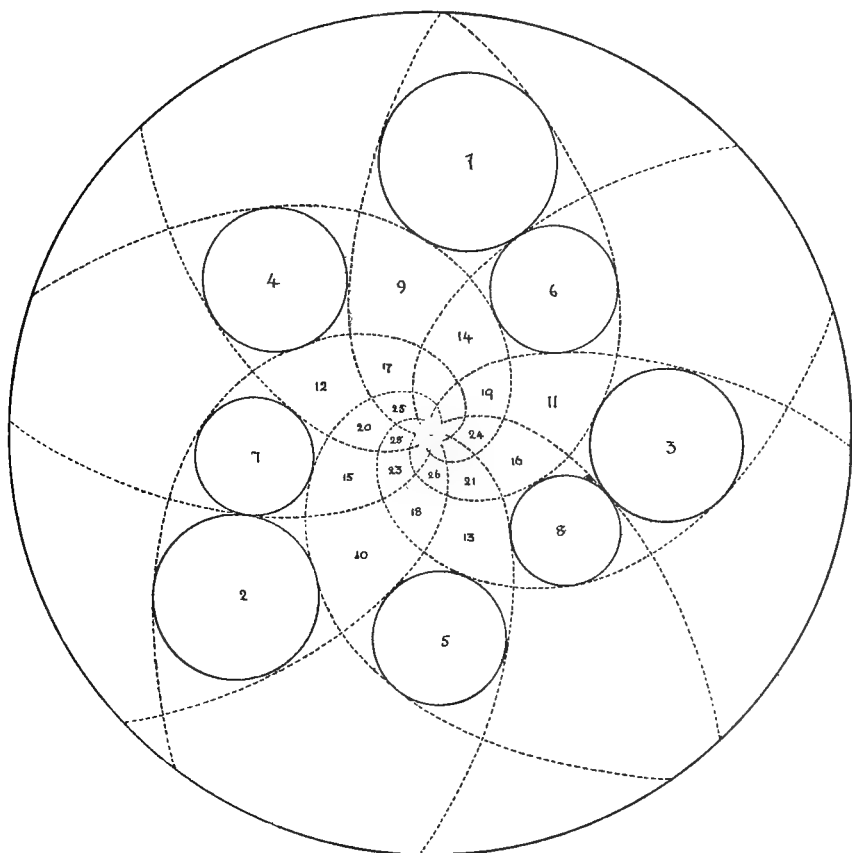
FIG. 35. Curve-system (5 + 8) : Fibonacci series. A full contact-cycle of eight members is represented by circular primordia.

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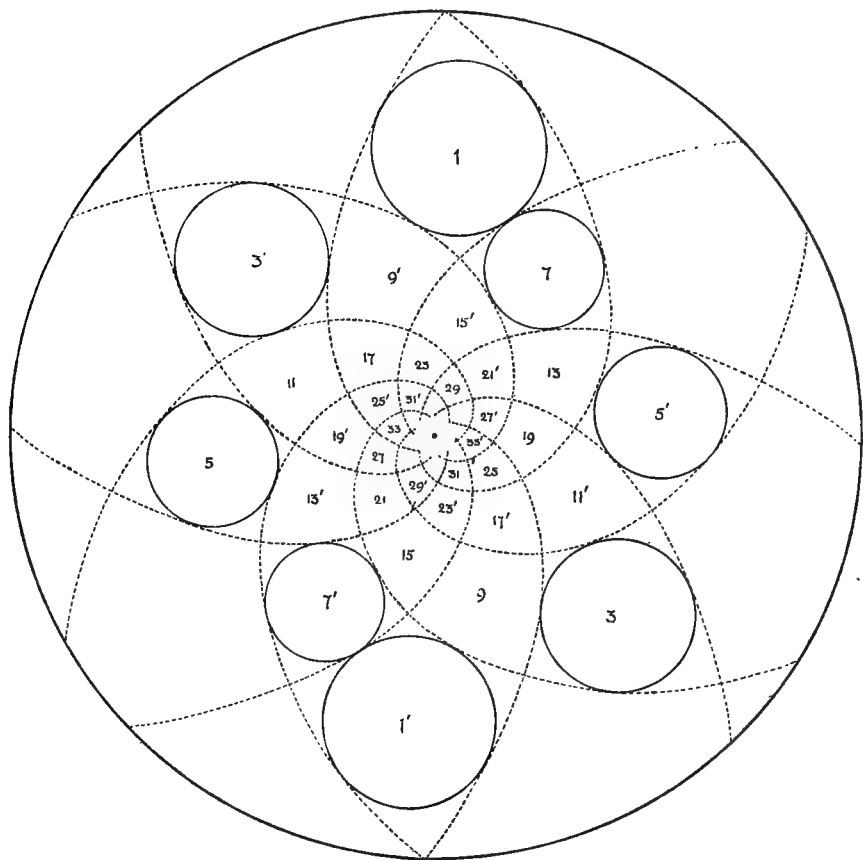
FIG. 36. Curve-system (6 + 8) : Bijugate type. Contact-cycle as in previous figure.

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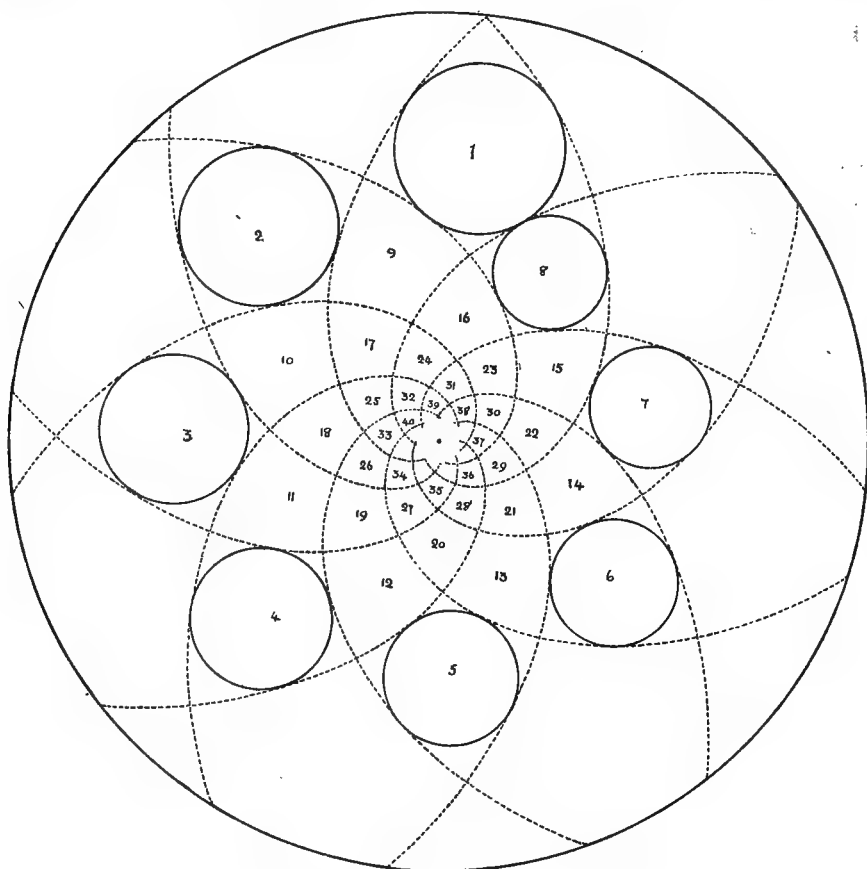
FIG. 37. Curve-system (7 + 8) : anomalous type.

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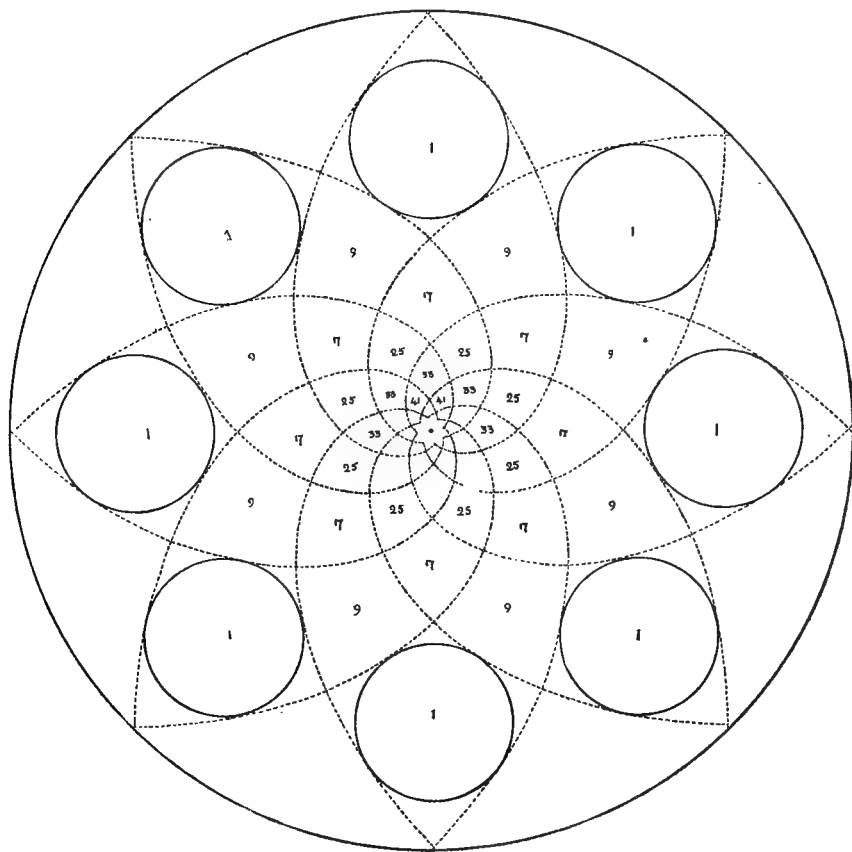
FIG. 38. Curve-system (8 × 8): symmetrical type.

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
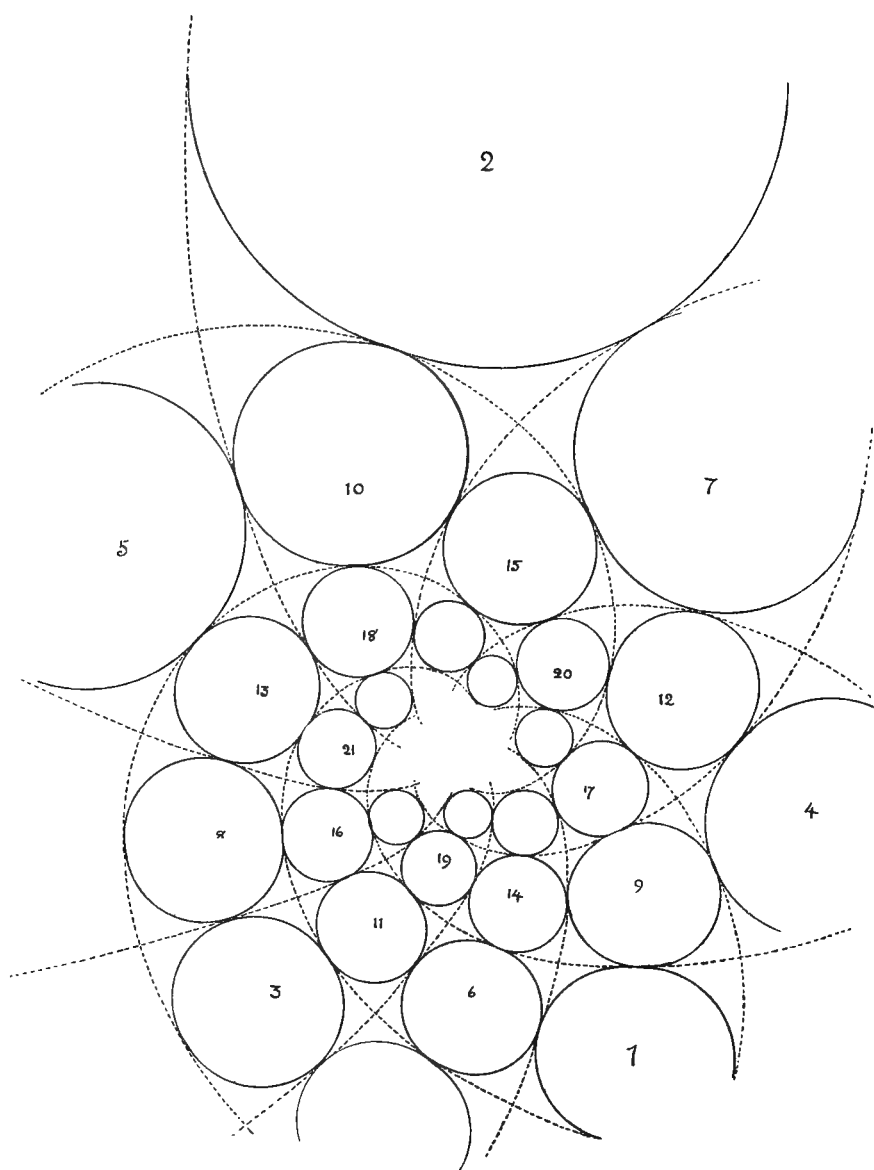
FIG. 39. System (5 + 8): eccentric construction in the plane of No. 2.

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? and

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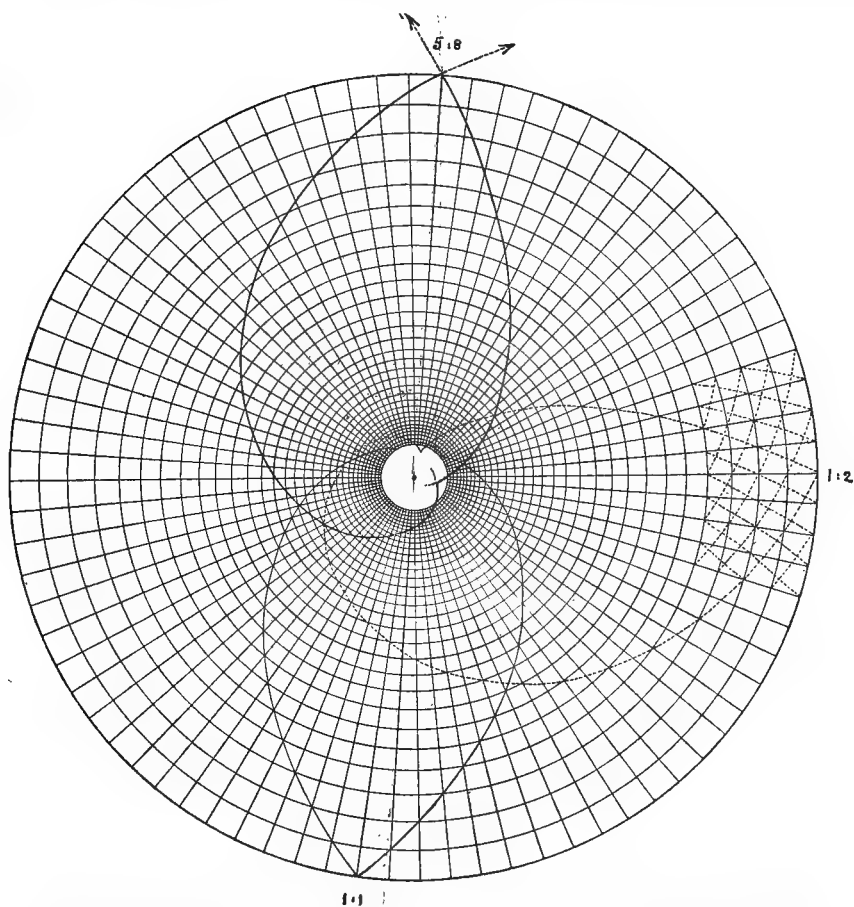
Fig. 40. Scheme for Uniform Growth Expansion: a circular meshwork of quasi-squares. Symmetrical construction from which asymmetrical homologues are obtained by the use of logarithmic spirals.

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 it [1].

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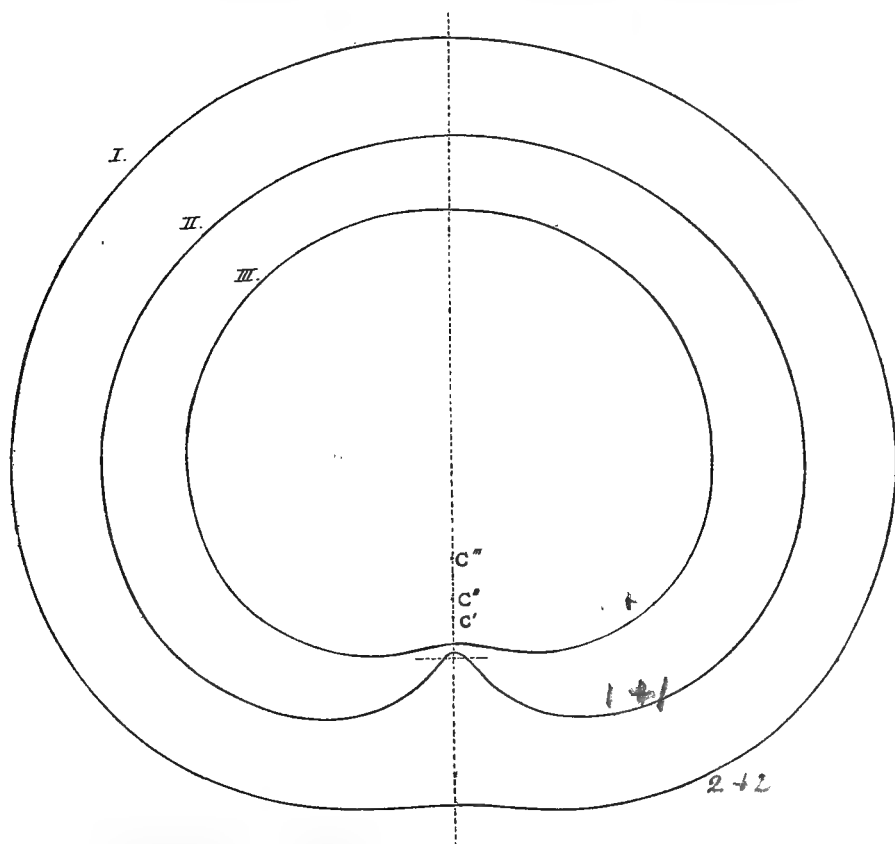
FIG. 41. Quasi-circles of the systems (2 + 2), (1 + 1) and (1 + 2) arranged for illustration in the plane of median symmetry. *C′, C″, C‴*, the centres of construction of the respective curves. (After E. H. Hayes.)

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 correct-
ness 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, *anisophyllous* structure, although the free appendage is *isophyllous*, bilaterally symmetrical, and flattened in a horizontal plane [1]. 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 system [2].

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 proto-plasmic 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 seg-mentation 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.

On the Relation of Phyllotaxis to Mechanical Laws.

By

Arthur H. Church, M.A., D.Sc.,
Lecturer in Natural Science, Jesus College, Oxford.

PART I.

CONSTRUCTION BY ORTHOGONAL TRAJECTORIES.

I. Introduction.

In the doctrine of Metamorphosis and the enunciation of the Spiral Theory we have handed down to us two remarkable generalizations which, originating in the fertile imagination of Goëthe, have passed through the chaos of Nature Philosophy and emerged in a modern and purified form, quite different from their primary conception, to form the groundwork of our present views of Plant morphology.

That leaves are usually arranged in spiral series had long been recognized by botanists; but it was left for Goëthe, in 1831, to connect the spiral-twining and torsion of stems, the spiral thickening of vessels, and the spirals of leaf-cycles into one ever-present " spiral-tendency " of vegetation.

The Spiral Theory proper, as applied to Phyllotaxis, owes its elaboration and geometrical completeness to Schimper and Braun (1830–1835), by whom it was worked out with such precision, and the ideas carried to their ultimate logical conclusion with such uncompromising vigour, that it still forms, in the early pages of text-books, the starting-point for our consideration of the relative positions of the members of the plant body.

A

And in this, of all older botanical generalizations, perhaps, it is alone worthy a place beside the Linnæan system of classification, that it first introduced methods of precise observation, record, and geometrical representation into the interpretation of the growth of the plant body as one whole organism, and thus paved the way for the classic morphological researches of Wydler, Irmisch, and Eichler.

To Hofmeister and Sachs, as founders of the modern school, the theory of Schimper and Braun, based on the observation of matured organisms, struck on the rock of development; but, while Hofmeister convinced himself of the utter inadequacy of the theory, he did not substitute any more comprehensive view, and Sachs did not investigate the matter at all deeply, regarding it as a mere playing with figures and geometrical constructions, of little interest except to those to whom it was practically useful.*

Further attempts at a more mechanical solution of the problems have been made by Schwendener ; and an admirable summary by Weisse in Goebel's *Organography of Plants* presents the methods adopted in explaining the phenomena observed by the action of the mechanical forces of contact-pressure.

The subject can, however, by no means be regarded as placed on a satisfactory footing.   It is clear, that if mechanical agencies come into play, they should be referable to the established laws of mechanics, capable of resolution into their component forces, and of diagrammatic representation in the different planes; while the part, if any, that is not mechanical, but due to some inherent " organizing property " of the protoplasm, requires to be clearly isolated from the products of known mechanical laws.

From a mechanical standpoint, it is perhaps in the diagrams that one feels most the absence of geometrical or mathematical constructions.   Thus Weisse, in using Schwendener's not at all

* Sachs, *On the Physiology of Plants*, Eng. trans., p. 499 : " For my part I have from the first regarded the theory of phyllotaxis more as a sort of geometrical and arithmetical playing with ideas, and have especially regarded the spiral theory as a mode of view gratuitously introduced into the plant, as may be read clearly enough in the four editions of my text-book."

Sachs, *Text-book*, edit. i., Eng. trans., p. 174 : " The treatment of the subject (*Parastichies*) is only of value to those who are practically concerned with phyllotaxis."

easily grasped simile of the twist on the girders of a span-roof, remarks that it is readily shown on a model but not on paper. When to this is added the puzzling results of abnormal cases, the general feeling left is that the mechanical forces are so well under the control of the living protoplasm of the plant that they may or may not act in any given case.*

Even if the diagrams and observations here recorded have no permanent value, it is hoped that they may tend to revive an interest in the methods of plotting out what may be termed architectural studies of vegetable life.

PHYLLOTAXIS.

By the oldest botanists the arrangement of leaves in series which formed alternating rows, when viewed horizontally or vertically, was very aptly described by the term " Quincuncial," from the analogy of the familiar method of planting vines in the vineyard (Daubeny, *Lectures on Roman Husbandry*, 1857, p. 152). Though such a diagonal pattern was produced by the indefinite multiplication of the quincunx (V), no reference to any special number (5) was implied, and all cases of spiral phyllotaxis and the great majority of whorled clearly come under this wide generalization † (Fuchs, *De Historia Stirpium*, 1542).

A more detailed classification appears to have been first proposed by Sauvages in 1743 (Sauvages, *Mémoire sur une nouvelle Méthode de Connoitre les Plantes par les Feuilles*, 1743).

* Goebel, *Organography of Plants*, Eng. trans., Weisse, p. 75.

Schwendener, *Mechanische Theorie der Blattstellungen*, 1878, p. 12 : "Die Schumann'schen Einwände gegen meine Theorie der Blattstellungen," *Berichte König. Preuss. Akad. Wiss.*, Berlin, 1899, p. 901.

† The view put forward by Fuchs, that the quincunx (V) was formed by halving the X, is not endorsed by modern authorities ; the 5-dot arrangement of a dice-cube being a more possible primitive form.

This original signification of the term *Quincuncial* was revived by Naumann in 1845 ("Ueber den Quincunx als Grundgesetz der Blattstellung vieler Pflanzen"). From observations on *Sigillaria, Lepidodendron*, and *Cactus* stems, he formulated a hypothesis of ridge and furrow construction, each ridge of a cactus being a row of the Quincuncial system.

Four types were established: the cases of opposite leaves, whorled, alternate and scattered (*feuilles éparses*) respectively; the definition of the last named being that it included all instances in which the members were arranged in no constant order.

Linnæus scarcely went farther than this. In his *Philosophia Botanica*, 1751, the types are increased to nine; *Dispositio sparsa* being extended to *Conferta, Imbricata,* and *Fasciculata* : the definition of *sparsa* being again "sine ordine."

Bonnet first determined a *spiral* arrangement, and his observations contain the germs of all subsequent spiral theories (*Recherches sur l'usage des Feuilles dans les plantes,* 1754, p. 159).

He classified leaf arrangement according to five types:

      (1) Alternating,
      (2) Decussate (*Paires croissées*),
      (3) Whorled,
      (4) Quincuncial,
      (5) Multiple Spirals (*Spirales redoublées*):

the last two of these being the ones which present the essential points of interest.

Not only did Bonnet thus originate the spiral construction, but he claimed to have discovered the "final cause" of the arrangement of leaves, and his generalization, 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,*" has had a remarkably persistent influence on subsequent investigators.

Omitting this physiological standpoint, the morphological generalizations of Bonnet were sufficiently striking. In this fourth type, he included the true $\frac{2}{5}$ spiral as we now understand it, in which a spiral makes two revolutions to insert five members, thus ultimately producing five vertical rows on the axis; and this arrangement he checked on sixty-one species of plants. The term *quincuncial,* thus defined, became limited to a special type of spiral phyllotaxis quite apart from its original signification. He further noted the tendency of the $\frac{2}{5}$ phyllotaxis to vary to vertical rows of 3 or 8 on the same species: the variation in the rise of the spiral,

right or left, in individual cases; and the correlation of the $\frac{2}{5}$ arrangement with a 5-channelled stem.

The fifth type of " Redoubled Spirals " is of even greater interest, in that it contains the germ not only of the *parastichies* of Braun, but also of the *multijugate* systems of Bravais.

Only two examples were noted: *Pinus*, in which three parallel spirals of seven members each resulted in a cycle of 21 members, and *Abies*, in which five parallel spirals of eleven members each gave a total of 55. These latter observations are credited to Calandrini, who also drew the figures.

The lack of higher divergences appears to be due to Bonnet's preference for the longest leafy axes, and his special precautions to avoid the terminal bud as much as possible, since this did not give accurate results! Notwithstanding this, he saw quite clearly in the case of the Apricot (p. 180) that successive $\frac{2}{5}$ cycles were really not vertically superposed, and that, in fact, the first members of each successive cycle also formed a spiral, and so in practice no leaf was vertically superposed to another on the same axis. This he regarded, not as the expression of any fault in the theory, but as a confirmation of his law, since such a *secondary displacement* would give room for the proper function of every leaf.

Subsequently, arrangements in which eight and thirteen parallel spirals could be counted (the latter in the staminal cone of *Cedrus*) were distinguished by De Candolle (A. P. de Candolle, *Organographie Végétale*, 1827, vol. i. p. 329). ·

From such a medley of observations on vertical rows and parallel spirals, the more modern theory of phyllotaxis was evolved by the genius of Schimper and Braun.

The vertical rows become " *orthostichies*," the parallel spirals " *parastichies*," the number of leaves between two superposed members becomes a " *cycle*," and these are tabulated in a series :—

$$\tfrac{1}{2}, \quad \tfrac{1}{3}, \quad \tfrac{2}{5}, \quad \tfrac{3}{8}, \quad \tfrac{5}{13}, \quad \tfrac{8}{21}, \quad \text{etc.,}^{*}$$

* The properties of the Schimper-Braun series, 1, 2, 3, 5, 8, 13, etc., had long been recognized by mathematicians (Gerhardt, Lamé), and appear to have been first discussed by Leonardo da Pisa (Fibonacci) in the 13th century.

Kepler, in 1611, speculated on the occurrence of these numbers in the vegetable kingdom, and went so far as to suggest that the pentamerous flower owed its

from the central commonest type ($\frac{2}{5}$), the quincuncial system of Bonnet. The essence of the Schimper-Braun theory, however, consists in the fact that these ratios of the numbers of members (denominator) to the turns of the spiral (numerator) being thus expressed in fractional form, become reduced to angular measurements expressed in degrees of arc (the *divergence*), and that a single *genetic spiral* controls the whole system.

When expressed in degrees, these divergences show an oscillation between $\frac{1}{2}$ and $\frac{1}{3}$, or 180° and 120°, towards a central station of rest, an angle to which the term "*ideal angle*" was applied by Schimper.*

$$\text{Thus, } \frac{2}{5} = 144°$$
$$\frac{3}{8} = 135°$$
$$\frac{5}{13} = 138° \ 27' \ 41''\cdot54$$
$$\frac{8}{21} = 137° \ \ 8' \ 34''\cdot28$$
$$\frac{13}{34} = 137° \ 38' \ 49''\cdot41$$

$$\frac{21}{55} = 137° \ 27' \ 16''\cdot36$$
$$\frac{34}{89} = 137° \ 31' \ 41''\cdot12$$
$$\frac{55}{144} = 137° \ 30' \ \ 0''$$
$$\text{"Ideal angle"} = 137° \ 30' \ 27''\cdot936$$

It will be noticed that the differences become extremely minute in the higher fractions, and that beyond $\frac{5}{13}$ the difference is much less than one degree of arc; an angle quite impossible of observation on most plants or of accurate marking on a small diagram.†

No satisfactory attempt could be made at measuring the angles; in fact, the brothers Bravais came to the conclusion that within the error of observation all these higher divergences might be due to a constant angle.‡

structure to the fact that 5 was a member of the series.   *Cf.* Ludwig, "Weiteres über Fibonacci-curven," *Bot. Centralb.* lxviii. p. 7, 1896.

* It will be noted that Schimper's formulæ are based on the type of the quincuncial system ($\frac{2}{5}$) of Bonnet. The construction proposed by the latter, with the co-operation of the mathematician Calandrini, was that of a helix drawn on a cylinder. Such a system transferred to the plane representation of a floral diagram, become a spiral of Archimedes, in which the sixth member falls on the same radius vector as the first. The parastichies differing by two or three respectively will similarly be Archimedean spirals. The truth of these systems will therefore stand or fall acording as constructions by means of spirals of Archimedes, derived from a consideration of adult cylindrical shoots, will explain the facts observed in the actual ontogeny of the members.

† *Cf.* Bravais, *Ann. Sci. Nat.*, 1837, pp. 67–71.

‡ *Cf.* C. de Candolle, *Théorie de l'angle unique en Phyllotaxie*, 1865.

This clearly formed the weakest point of the theory. It is quite useless to take angular measurements as the basis of a theory when they cannot be checked.

Again, in considering the common quincuncial ($\frac{2}{5}$) type, it is quite easy to suppose that if five members developed in spiral series were left isolated on a stem, they would space themselves out at equal angles of 72° if they developed symmetrically: but it does not follow that they were produced at exact successive angles of 144°, although this number may have been approximated.

It is, in fact, a matter of ready observation, as Bonnet noticed, that in none of the cases usually described as $\frac{2}{5}$, and continued for several members, does the sixth member come exactly over the first, but rather falls a little earlier in the gap between 1 and 3. The longer the internodes, the nearer it appears to so come, but the range of error may clearly be very large: thus, to form the 6th leaf of a $\frac{2}{5}$ cycle the spiral should have rotated $5 \times 144 = 720°$; the nearest 6th leaf of any other cycle is that of the $\frac{5}{13}$, to form which the spiral rotates 692°. In a given case, therefore, when it becomes necessary to decide whether the cycle stops at $\frac{2}{5}$, or is continued on to $\frac{5}{13}$, a range of error as great as $\frac{28}{2} = 14°$ requires to be negotiated. Such a range in a system which in higher values comes down to minutes and seconds does not tend to render the original spiral theory very acceptable.

The determination of the fractional value depends, therefore, since angular measurements are out of the question, on the determination of a member vertically superposed, to one taken as a starting point. The theory of Schimper and Braun really stands or falls, then, with the observation of "*orthostichies*," that is to say, according as a leaf which appears to stand vertically above any given one is actually so. Of this, again, proof is impossible: the very fact that in going up the series to count the divergence on a specimen, a nearer and nearer vertical point is obtained at every rise, suggests that the one ultimately selected is only an approximation, the eye being as incapable of judging a mathematically straight line as it is of measuring an angle to fractions of a degree.

That orthostichies tend to become *curviserial* in the higher divergences was more fully recognised by Bravais, and very in-

genious constructions were adopted by Braun and Eichler to adapt
the "obliquely vertical" rows of stamens in several Ranunculaceous
flowers as true orthostichies.   But it is clear that no sharp line
can be drawn between parastichies and orthostichies when once the
latter become curved.

Hofmeister, who approached the subject with the most open mind,
came nearest the truth in formulating the statement that, in the
bud, a new member always arises in the widest gap between two
older ones.   That the logical consequence of this would be that no
member would ever be vertically superposed to another, nor again
would it be so if developed at the "ideal angle," has been duly
recognized.   But such conclusions have always been slurred over by
supporters of the spiral theory : either the observations must be
imperfect, or the specimens must have suffered from torsions or
displacements; the remarkable series of mathematical fractions
could not possibly be wrong: the perfect accuracy of the "ideal
angle" could not be expected of the plant : the object to be attained
namely, the best possible distribution of assimilating surface being
sufficiently approximated at a comparatively low divergence.*

When once phyllotaxis is committed to this series of fractions,
expressing actual ratios of angular measurement, all deductions
from the mathematical properties of such a series naturally follow.
The remarkable superstructure therefore stands or falls according
to the correctness of the original series, based, as already noticed,

* *Cf.* Bonnet, 1754, p. 160 ; De Candolle, 1827, *Organographic Végétale*, vol.
i. p. 331.

Cf. Chauncey Wright, 1871.   " On the uses and origin of arrangements of
leaves in plants" (*Mem. Amer. Acad.* ix. 387, 390).   The continuation of this
theory of leaf distribution initiated by Bonnet, affords a remarkable example of
the method of biological interpretation of phenomena.   Because a spiral series
gives a scattered arrangement of leaves and is very generally met with, it
does not at all follow that such a scattered arrangement is beneficial or at all an
aim on the part of the plant : nor again that the "ideal angle" would give
the ideal distribution.   It is clear that in the intercalary growth of petiole-
formation the plant has a means of carrying leaves beyond their successors,
whatever the phyllotaxis may be ; while if the ideal angle of a spiral phyllo-
taxis becomes the ideal angle of leaf-distribution, the formation of whorled
series from primitive spirals, to say nothing of secondary dorsiventral systems,
becomes curiously involved.

on orthostichies which cannot be proved to be straight and angles which cannot be measured.

Thus, if the angle of divergence within one cycle is constant, a transition from one cycle to another of different value must involve a special angle at the point of transition. To meet this difficulty the theory of "prosenthesis" was added to the original conception by Schimper and Braun; a hypothesis again incapable of proof by any actual measurements on the plant.*

Prosenthesis was also called upon to explain the alternation of cycles in the common type of flower; and, in the same way, in the formation of whorls of foliage leaves which usually alternate, prosenthesis was required at every node.

Still more remarkable were the constructions adopted to explain the "obliquely vertical rows" of stamens in the flowers of certain Ranunculaceæ. In order to bring these into line with "orthostichies," peculiar transitional divergences were adopted; a $\frac{3}{8}$ spiral *e.g.* might, with a tendency to approach $\frac{5}{13}$, give a somewhat larger angle to every new cycle; and, owing to this special form of prosenthesis, the true orthostichies would take an oblique position, in this case, along the course of the genetic spiral.†

Once, however, it is admitted that such transitional divergences may render orthostichies oblique, the whole theory becomes considerably weakened, since no clue is given to the causes which may produce such an effect in one case and not in another; while the fact that what it has been the custom of older writers to call orthostichies should prove to be really a little curved, does not at first strike the observer as necessarily affecting the validity of the original hypothesis.‡

On the other hand, with all its faults, the definite notation of the Schimper-Braun theory, and the brevity and apparent simplicity with which it sums up complicated constructions, is so closely interwoven with our whole conception of the subject, that it becomes

* Eichler, *Blüthendiagramme*, i. p. 14.
† Eichler, *Blüthendiagramme*, ii. p. 157.
‡ Sachs, *Physiology*, Eng. trans., p. 497. "The theory of phyllotaxis, with its assumption of the spiral as a fundamental law of growth, has, to the great injury of all deeper insight into the growth of the plant, established itself so firmly that even now it is not superfluous to show up its errors point by point."

extremely difficult to take up an unbiassed standpoint, or recast the matter in a new phraseology; while to deny the actual existence of the genetic spiral otherwise than, as Sachs has suggested, an unimportant accessory of the construction, savours of direct heresy.

The criticism of Sachs, which strikes at the root of the theory of Schimper and Braun as applied to living organisms, applies equally well to the work of other observers, and requires to be constantly borne in mind.*

Because, writes Sachs, we can describe a circle by turning a radius around one of its extremities, it does not follow that circles are produced by this method in nature. Because we can draw a spiral line through a series of developing members, it does not follow that the plant is attempting to make a spiral, or that a spiral series would be of any advantage to it. Geometrical constructions do not give any clue to the causes which produce them, but only express what is seen, and this subjective connection of the leaves by a spiral does not at all imply any inherent tendency in the plant to such a system of construction.†

Much of this, again, applies to the methods adopted by Schwendener. Because an empirical system can be forced by pressure into a condition resembling that obtaining in the plant, it does not follow that a similar pressure acting on a similar system is in operation in the plant itself.

Schwendener,‡ it is true, made a great advance in dealing with solid bodies and spheres, rather than the abstract geometrical points of the Schimper-Braun theory; and, so far, Goebel is undoubtedly right in stating that further research must be conducted along the lines laid down by him. But at the base of all Schwendener's constructions lies the fact that he begins by assuming the fractional series of Schimper and Braun, and then arranges a mechanism to convert these into systems more in accord with what is actually observed in the plant.

* Sachs, *History of Botany*, Eng. trans., p. 168.

† *Mechanische Theorie der Blattstellungen*, 1878.

Cf. Airy, *Proceedings of the Royal Society*, 1874, vol. xxii. p. 297, for a very similar hypothesis of pressure on actual primordia without reference to the actual structure of the growing point.

‡ Goebel, *Organography*, Eng. trans., p. 73.

It is clear, however, that whatever subsequent alterations are made in the system, the construction remains fundamentally that of Schimper and Braun, and must stand or fall with the truth of the premises which govern the original fractional series; and these, as has been pointed out, are extremely vague, and have to a great extent been rejected by Hofmeister and Sachs.

Contemporaneously with Schimper and Braun, the problems of phyllotaxis were being attacked by the brothers A. and L. Bravais, with in some respects identical results.*

Very scant justice has been done by Sachs † to the remarkable work of these French observers.   The parts in which they appeared to agree with Schimper and Braun have been accepted, those in which they differed have been rejected. It is not too much to say that in the latter case they were wholly correct, and in the former they came under the same erroneous influences as the rival German school.

Thus, Sachs sums up by saying that their theories presented the defects and not the merits of the Schimper-Braun system, in that they made use of mathematical formulæ to an even greater extent without paying attention to genetic conditions, and the whole was "much inferior as regards serviceableness in the methodic description of plants to the simple views of Schimper."

It is evident that Sachs' distaste for the whole subject prevented him from going into the matter very carefully, as the first thing that strikes the reader is the very definite attempt made by the Bravais to actually measure the angles and confirm their results experimentally. It was owing to failure in this respect that they fell back on the method of orthostichies and on this basis erected very consistent hypotheses. When orthostichies obviously failed, they approached the actual truth much nearer than Schimper and Braun. They thus distinguished two kinds of spiral phyllotaxis (1), that in which orthostichies were present and *rectiserial*; (2) that in which the so-called orthostichies were obviously *curviserial*. The former applied to cylindrical structures and was so far identical with Schimper's theory, which was also based on mature cylindrical

* *Ann. Sci. Nat.*, 1837, p. 42.
† *History of Botany*, Eng. trans., p. 169.

organs ; but, in the latter, they pointed out that the axis was often conical or circular : in such case the straight orthostichies were wanting and successive cycles were not accurately superposed. More complete acquaintance with the structure of growing-points would have shown them that the first case was wholly unnecessary, and that the second hypothesis, based on a cone which might be flattened to a circular disk, was alone required. Again, in common with Schimper and Braun, they shared the view that the lateral members were equal in bulk, or might be expressed by points, when in point of fact they present in development a gradated series. They, however, arrived safely at the conclusion that in such systems the construction could not be expressed by a fractional divergence, but only by the number of interesting parastichies (sinistrorsum and dextrorsum), and the figure drawn for the theoretical structure of a Composite inflorescence is very nearly correct, although its method of construction (probably by modified Archimedean spirals) is not described. Still more remarkable was the care with which they worked out the multijugate types, in which the fractional expression was divisible by a common factor (2–3), and thus clearly pointed to the presence of two or more concurrent genetic spirals, a case not contemplated by the spiral theory of Schimper and Braun.

Restricted to the doubtful method of orthostichies, the Bravais followed Schimper and Braun in the elaboration of other sets of divergence fractions.*

Thus if $\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}$, etc., pointed, as stages of a continuous fraction, to an ideal angle of $137°\ 30'\ 28''$, why might not there be a complementary system $\frac{1}{3}, \frac{1}{2}, \frac{2}{5}, \frac{3}{7}, \frac{5}{12}$ pointing to $151°\ 8'\ 8''$? As also $\frac{1}{3}, \frac{1}{4}, \frac{2}{7}, \frac{3}{11}$, etc., leading on to an ideal angle of $99°\ 30'\ 6''$, and $\frac{1}{4}, \frac{1}{5}, \frac{2}{9}, \frac{3}{14}$, etc., to $77°\ 57'\ 19''$!

It is clear that by such hypotheses any fraction that can be counted may be regarded as a member of some system ; and, as Sachs has pointed out, this degenerates into mere "playing with figures"; while no progress along such lines is possible when a physiological reason is asked for. Still, these formulæ were founded

* Bravais, *Ann. Sci. Nat.*, 1837, p. 87 ; Van Tieghem, *Traité de Botanique*, p. 55, 1891.

on direct observations of plants, and the results are so far logically carried out along Schimper-Braun lines of argument.

If these arrangements are regarded as the *reductio ad absurdum* of the whole subject, it follows that the original premises are possibly incorrect. It is so far only necessary to point out that these cases are relatively much less numerous, and occur in plants which exhibit marked adaptations to special biological environment, or, in modern phraseology, are markedly xerophytic, as for example, *Dipsacus, Sedum, Pothos, Bromelia, Cactaceæ.*

By adopting the following construction, and using the usual terminology, a very plausible diagram, which conveys a useful summary of the Schimper-Braun theory, may be plotted out (fig. 1). If it be granted that, given a constant type of lateral member, the phyllotaxis would rise, as expressed in the fractional series, with successive increase in the diameter of the axis, it might also follow that it would fall on a constant axis if the members increased in bulk, or rise if they were diminished, according to the number of members which would fill a cycle round the stem.

Fig. 1.—General scheme for the orientation of the cycles of the Schimper-Braun hypothesis.

Again, since members pack more or less together, spheres to a certain degree extending into the rows adjacent to them, while rhomboid figures each press one half their length into adjacent cycles ; and since, to take the general case, the plant commences growth from two symmetrically placed cotyledons (divergence $\frac{1}{2}$), it would pass on to a spiral arrangement in the simplest manner by placing one member on one side and two on the other (= divergence $\frac{1}{3}$). With no further increase in the
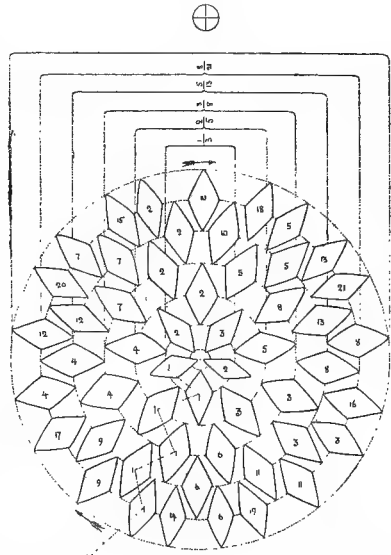
bulk of the axis, or with increase in both axis and lateral members definitely correlated, the phyllotaxis would remain $\frac{1}{3}$. If a further rise took place, the five gaps would be filled by the five members of a $\frac{2}{5}$ cycle, and in the same manner in successive cycles, two new members being always added opposite the larger gaps corresponding to the members of the last cycle but one, and thus each new cycle would equal the sum of its two predecessors, and the rise in divergence would be repeated ontogenetically in every individual.

The members of each cycle would have their appropriate angular divergence (although this is only approximated in the figure), and for a constant type of member such an ascending series would be produced with an increased diameter in the stem ; lateral branches, proceeding from two symmetrically placed prophylls, would take on a spiral construction according to their relative bulk.

The whole figure is orientated for the $\frac{2}{5}$ position, so uniformly present in the quincuncial calyx, and the members numbered in this relation, so that No. 2 is median posterior.

An enormous number of facts may be collected in support of such a construction and incorporated with it without, however, necessarily establishing its accuracy. Thus the orientation of a $\frac{3}{8}$ cycle with regard to a $\frac{2}{5}$ is in all cases exactly as shown. For example, in *Helleborus foetidus*, the flower possesses a $\frac{2}{5}$ calyx with normal orientation, and eight nectary petals of a $\frac{3}{8}$ series, of which most commonly 1–5, 6, 7 are present. The missing ones, 8, 7, 6, as the case may be, always leave gaps in the positions marked by these numbers with absolute constancy. The relation of two cycles having been established, the other cycles may be regarded as following the same plan, and may readily be numbered from the divergence scheme—No. 1 being given by line which zigzags through No. 1 of successive cycles to approach the "ideal angle."

It may be noted that the $\frac{1}{3}$ spiral gives the odd member anterior, the typical position in the case of trimerous monocotyledonous flowers, while the $\frac{1}{2}$ cycle falls transversely, as in the case of the two prophylls.

Although a multitude of facts may be fitted into such a scheme,

and the relationship of members is thus readily tabulated and placed in diagrammatic form, as in the construction of floral diagrams, it affords · no explanation of the fact why, for example, a $\frac{2}{5}$ divergence may be continued indefinitely, and then, when it does rise, passes into a $\frac{3}{8}$ or even directly into a $\frac{5}{13}$, as in the construction usually given for the nectaries of *Helleborus niger.* One begins to regard with suspicion the convention which infers from five members a $\frac{2}{5}$ spiral, and from thirteen members a $\frac{5}{13}$ spiral, while a fall to five carpels may be interpreted as a reversion to a $\frac{2}{5}$ spiral again. The conventions do not explain anything; and it is not clear, if angular distances cannot be checked, what criterion can distinguish between five members of a $\frac{2}{5}$ spiral and the first five, for example, of an $\frac{8}{21}$ series.

Schwendener in his constructions accepts the divergences as standard quantities, and proposes figures of transition in which the varying bulk of the elements is taken into account. The point of view adopted here will be that, in the case of normal and phylogenetically primitive modes of growth, the divergences themselves convey an erroneous impression, and that all theories which include their acceptance must necessarily fall to the ground.

Nothing is more striking, in dealing with the subject of phyllotaxis, than the large number of hypotheses put forward which are almost equally incapable of direct proof or disproof; and the difficulty of the problem consists in determining a sure foundation on which subsequent theories may be elaborated.

The hypothesis of Schimper and Braun does not satisfy the demands of modern investigation, in that its premises do not admit of strict observation and measurement, and for similar reasons Schwendener's views on mechanical contact-pressures are incapable of direct proof.*

. That such contact-pressures exist, and operate to a very considerable extent in producing secondary changes, is undoubted; but it does not follow that they are so pre-eminently important and lead to such great disturbances of the original construction, since it is possible that by being equally distributed the disturbing effect

---

* *Cf.* K. Schumann, *Morphologische Studien*, Heft 2, 1899, p. 312; C. de Candolle, *Considerations sur l'étude de la Phyllotaxie*, 1881, p. 27.

would be inappreciable. The objection to Schwendener's theory is then, that it superimposes a second doubtful hypothesis on the original unsatisfactory one of Schimper and Braun. On the other hand, if the subject can be dealt with *ab initio* from a new stand-point, it is not necessary to discuss the details of the conflicting observations of Schwendener and Schumann.

In the present paper an attempt will be made to base all deductions on a single hypothesis, the mathematical proposition for uniform growth, as that of a mechanical system in which equal distribution of energy follows definite paths which may be studied by means of geometrical constructions.

PLATE I.

FIG. 3.—The same plant cut transversely, and the leaves numbered in order from the centre.
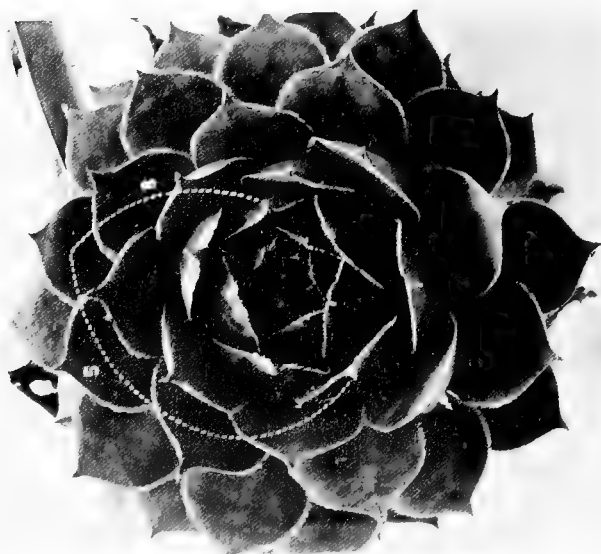
FIG. 2.—*Sempervivum calcaratum*, Hort. 60 mm. diameter; more obvious parastichies (5 + 8).

II. General Observations.

1. METHOD OF DETERMINING ORTHOSTICHIES.

As the difficulty of determining a vertical series increases with the length of the internodes, and may be complicated by possible torsion and irregular growth curvatures, a plant may be selected in which growth and subsequent displacements are obviously at a minimum.

A typical " rosette-plant," such as *Sempervivum*, affords suitable material: the leaves develop symmetrically and retain the positions impressed on them in the bud.

The plant presents, as a whole, the usual curved systems of intersecting parastichies, the most obvious being five in one direction and eight in the other (fig. 2 ; also fig. 4).

By a horizontal cut, the whole plant may be reduced to one plane, and, commencing at the centre, the leaves may be readily numbered in serial order of development from one to about fifty (fig. 3). A vertical row of leaves, or an *orthostichy*, should clearly appear in the section as a *radius* passing through the centre of the leaves, differing in number by the denominator of the fractional expression. The leaves 1, 6, 11, 16, etc., form a very obvious curve, so that $\frac{2}{5}$ is rejected ; the leaves 1, 9, 17, 25, etc., form an equally obvious curve in the opposite direction, hence $\frac{3}{8}$ is rejected. For the same reason, 1, 14, 27, 40 form a lesser curve, but still distinct enough to disqualify $\frac{5}{13}$. In 1, 22, 43 the curve hardly appears, and 1, 35 is possibly straighter, but further investigation is limited by the number of leaves.

A comparison of the closer and closer proximity of these curves

B

to a central ideal line, suggests most clearly that no orthostichy is really possible until the "ideal angle" is reached; that is to say, only at infinity will a leaf be found exactly on the same radius as 1. The series in the specimen is bounded by a few leaves, and so No. 22 is near enough for practical purposes, and the phyllotaxis is usually given as $\frac{8}{21}$; but there is no proof of its position over No. 1; on the contrary, a very strong presumption against the acceptance of any orthostichies at all.

2. Braun's Method of Determining Parastichies.
(*Pinus Pinea.*)

The ripened carpellary cones of *Pinus* afford useful permanent examples of spiral phyllotaxis. The large cone of *P. Pinea*, $5\frac{1}{2}$ inches by 3, is especially suitable for observation, and the smooth scales are large enough to be clearly numbered.

Such a cone is observed to consist of obliquely intersecting rows of scales (fig. 6-7), of which eight long curves intersecting thirteen shorter ones are the most obvious.

Since the cone may be regarded as built up of a certain number of oblique rows winding left, or again of a certain number of rows winding right, a complete cycle may be regarded as formed by taking one member from each of the two series. Thus in the case figured (fig. 7), the structure may be regarded as built up of—

I., of oblique rows of the type 1, 9, 17, etc., of which eight can be counted going all round the cone.

II., of rows 1, 14, 27, etc., of which thirteen can be counted.

III., of rows of the type 1, 22, 43, etc., of thich there are twenty-one.

In the first case, the scales will differ by eight, the number of the curves, in the second by thirteen, and in the third by twenty-one.

A simple method thus follows for numbering the scales in the serial order of their development (*genetic spiral*). By taking any given scale as one, the number of each one adjacent to it may be determined by counting round the cone the number of curves in

PLATE II.

Fig. 5.—*Pinus austriaca*, Link, dry expanded cone seen from below, parastichies (8 + 13).

Fig. 4.—*Sempervivum spinulosum*, curve system dotted (13 + 21).

.

the same sense with it, and by zigzagging from scale to scale the whole cone is numbered up. From a consideration of the parastichies of other systems, Braun* tabulated a series of fractions $\frac{1}{2}$, $\frac{2}{3}$, $\frac{3}{5}$, $\frac{5}{8}$, $\frac{8}{13}$, $\frac{34}{55}$, etc., complementary to those of Schimper's series of orthostichies. The method is strictly accurate, and clearly affords the only way of numbering up the members of a complicated spiral system when the lateral members retain their original close contact on a condensed axis.

However, as soon as attempts are made to bring the system of parastichies into line with that of orthostichies, difficulties arise. The system of $(8+13)$ parastichies corresponds in the Schimper-Braun theory to a phyllotaxis of $\frac{8}{21}$, but it is at once clear that 22 is not superposed to 1. The scale marked 35 is practically over it, and hence the phyllotaxis would be usually given as one stage higher, i.e. $\frac{13}{34}$, to fit which divergence it would be necessary to assume that the correct parastichies are those passing through 1, 14, 27, and 1, 22, 43 respectively. In other words, the steepest parastichies are to be taken as a guide. As in the preceding case of *Sempervivum*, however, there is no evidence that 35 is vertically superposed to 1 ; the figure, in fact, shows that it is only approximately so, and that if 56 were normally placed it might be nearer the vertical line. Owing to the sloping off of the cone, 56 is clearly well off the line, and 35 remains the nearest for practical purposes. There is no proof of its accuracy ; but by comparison with *Sempervivum*, the strongest presumption in favour of its being only an approximation, owing to the limited number of members on a cylindrical portion of the axis. There is certainly no clear justification for assuming any secondary displacements in order to save the theory.

In fact, there is only one mathematically accurate statement which can be made about such a construction, and that is, that taking four scales in contact, or making use of a rhomb of rhombs (e.g., fig. 7: 1, 9, 22, 14), the cone is composed of $(8+13)$ intersecting spirals, of which eight are longer and thirteen shorter.

Adopting the convention that the right-hand direction is that marked by the hand of a watch at 12 o'clock, the cone figured

* *Flora*, 1835, p. 157.

(fig. 6) shows eight right- and thirteen left-handed spirals. (Fig. 5 *vice versa*.) Reversing this expression for the position seen when looking down on the apex of the cone instead of up from below as in the figure, in order to express the cone in terms of a floral diagram, the constant becomes (8 L+13 R), this being in fact the actual terminology proposed by the brothers Bravais. The direction of the spirals, however, may vary from cone to cone, and the more essential point is that the lower number of the expression gives the number of the longer curves, so that the formula (8 long +13 short spirals) remains the only cone-constant about which there is no mathematical doubt. Braun's method marks a real advance in that it replaces the long genetic spiral, quite impossible of observation in high divergences, by short intersecting curves which may be readily and accurately counted in the highest series.

The closer the members, the more difficult the question of orthostichies becomes, the method of transferring a system of parastichies to fractional terms expressing an accurate angular divergence becomes conventional, and one is unavoidably brought into agreement with Bravais, that in such a case as *Pinus*, the parastichies are all-important and the orthostichies imaginary.

The tapering of the Pine cone, however, militates against its being taken as a type of a cylindrical system, and the method, as applicable to the whole series of divergences, requires to be tested on cylindrical axes.

3. PHYLLOTAXIS OF EUPHORBIA WULFENII, *Hoppe*.

Euphorbia Wulfenii, a handsome Spurge growing 5–6 ft. high, as cultivated in the Oxford Botanic Garden, affords excellent cylindrical stems on which, owing to delayed formation of cork, the leaf-scars remain and are well marked.

The flowering-shoots, bearing evergreen leaves, persist for 3–4 years, terminating in a compound inflorescence, without, however, producing a terminal flower.

Beyond the two cotyledons of the seedling, or the two prophylls of a lateral shoot, the phyllotaxis rises to a medium elevation, indicated roughly by $\frac{8}{21}$, and produces vegetative leaves on a

PLATE III.
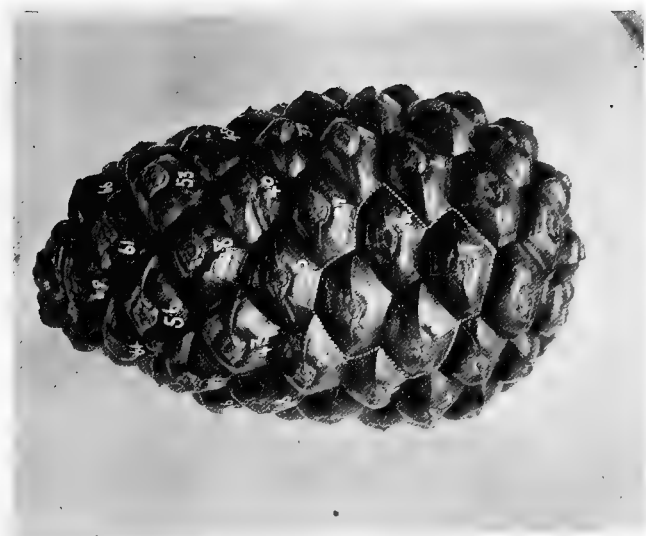
Fig. 7.—The same cone, 5½ inches long ; the scales numbered in order from a given 1 to 69.
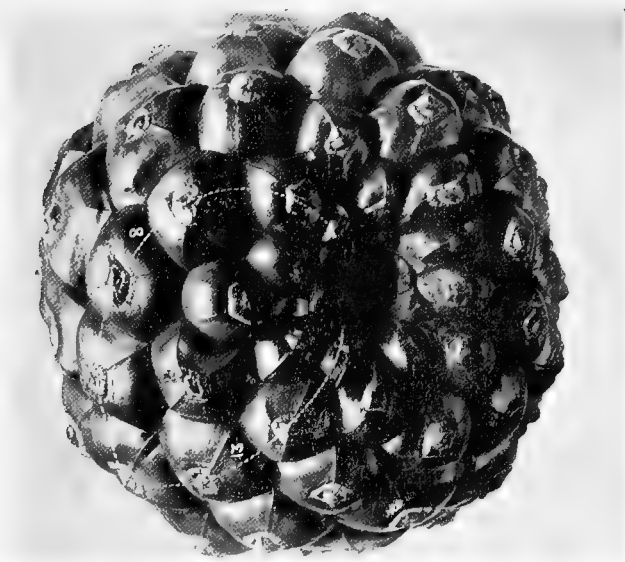
Fig. 6. — *Pinus Pinea*, L, closed cone, 3 inches diameter ; (contact-parastichies (8 + 13).

cylindrical stem for a distance of 3–4 feet or more before the end
tapers to the inflorescence.   Old flowering stems, cut in September
or October, when all the leaves have been shed, afford the best·
material.   On these cylindrical stems, owing to the absence of
winter-bud formation, the alternation of the seasons is shown by the
alternating approximation and separation of the leaf-scar cycles ;
the scars being closer together in autumn and fairly scattered in
spring.   The figure (fig. 8) represents a continuous portion of a
stem A, B, C, D, E, cut into four sections for convenience of illustra-
tion.   By using the method of parastichies on the spring area (A),
rhombs are readily noted formed by $(3+5)$ intersecting curves,
pointing to a $\frac{3}{8}$ phyllotaxis ; but the top member of the rhomb (9)
is not on the same vertical line as the bottom one, and the fraction
may therefore be higher.   On another piece (B, C) the same
rhombs are conspicuous, but another set may be marked out form-
ing $(5+8)$ curves of a $\frac{5}{13}$ phyllotaxis, but the top member of the
rhomb is again not vertically superposed to the bottom one.   On a
third piece (C, D) the same rhombs may be traced, or a steeper
series due to $(8+13)$ curves of $\frac{8}{21}$ type.   The top member is again
not in vertical series.   The stem is erect and contains little wood,
there is no sign of torsion on it, but the phyllotaxis, as defined by
the observation of orthostichies, seems ever elusive.   In the same
way still steeper curves may be located, as in D, E, where $13+21$
point to a $\frac{13}{34}$ system, and, given a long cylinder, they may be made
as steep as one likes ; as soon as the eye becomes accustomed to one
set, a still steeper may be seen.   It becomes clear that the curves
may be carried the whole length of the stem before the series comes
to a compulsory end.   This range was short in the Pine cone ; in the
cylinder it becomes indefinitely prolonged, a leaf accurately super-
posed to No. 1 being, in fact, only reached at some quite indefinite
station, although a nearer approach is gained at every rise of the
phyllotaxis series.   Thus the actual expression given becomes a
convention, since the ever-steepest curves pass beyond the limit of
observation.   These are the facts, but what do they mean ?

It is clear that the phyllotaxis fraction, whatever numerical
value is given to it, rises in the series as the axis is telescoped,
and falls as it is lengthened.   In fact, if a high phyllotaxis be

plotted out on a rubber-tube, and this greatly extended, it can be made to fall as low as one pleases. The mechanical effect of such tension or compression has been noted by Schwendener and Weisse.

Now, in this plant, the expansions and contractions of the system are due to varying rates of growth in the main axis. The spiral itself is constant and the same genetic spiral runs uniformly through the whole shoot, including different sets of parastichy curves, which, when marked out along the axis, present the appearance of a spiral spring expanded and contracted at different points.

The actual arrangement of the members on the stem is, in fact, here quite secondary; varying phyllotaxis phenomena are produced by varying rates of growth, a conclusion already reached by Bravais from the study of the rosette of *Sempervivum* and its flowering axis. The spiral arrangement is not an end at which the plant is aiming, but the mere retention of a uniform system impressed on it in the terminal bud.

It follows, then, that phyllotaxis is the obvious and visible expression of more obscure phenomena in the growing apex, and must be referred *to the first Zone of Growth*, since in passing through the Zone of Elongation it may be fundamentally altered in appearance.

Confirmation of the view that the spiral is only the relic of the effect of certain agencies at the growing point, and is not directly essential to the welfare of the plant, is shown by the general occurrence of cases in which the originally spirally arranged leaves become secondarily dorsiventral in arrangement by torsion of the leaf-stalks; *i.e.*, the effect of the spiral becomes secondarily corrected as soon as it becomes a distinct disadvantage to the plant.

It follows again that, for any spiral leaf arrangement that has passed through this second zone of elongation, no expression which is not a purely arbitrary and conventional one can be formulated.*

Phyllotaxis is to be studied in the growing apex itself, or in structures which have undergone so little elongation that the

* Transverse sections of the apices of shoots of *Euphorbia Wulfenii* (cf. figs. 90, 91) show systems in which the contact parastichies are $(8+13)$, $(5+8)$, and in very weak shoots $(3+5)$.

PLATE IV.

FIG. 9.—*Cynara Scolymus*, L. Involucral scales from below. Capitulum 8 inches in diameter.
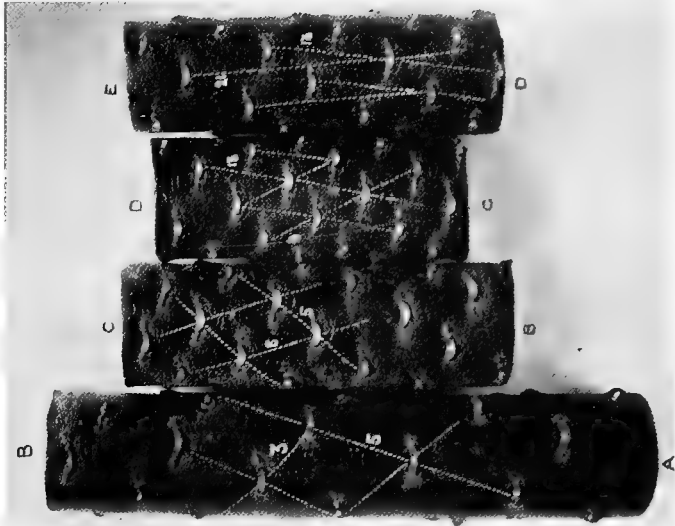
FIG. 8.—*Euphorbia Wulfenii*, Hoppe. Stem 15 mm. in diameter; various systems of parastichies on a continuous portion of the axis A, B, C, D, E.

individual members remain in their original close lateral contact. It is impossible to exaggerate the importance of the acceptance of such a generalization. At one sweep it clears away all the foundations of the Schimper-Braun theory, and all other formulæ based on the study of mature cylindrical organs with isolated members, which from the time of Bonnet have been regarded as the types of construction, and for which expressions were required by descriptive systematists.*

4. Phyllotaxis of Cynara Scolymus, *L.*

The great inflorescence heads of the cultivated Globe Artichoke produced an involucre of protective scale leaves 8–9 inches in diameter in the expanded head. These form a definite spiral series starting from a very low divergence on the elongated main axis and reaching a very high one at the periphery of the disk. The scales are large and the insertion of the lower one quite clear, so that these may be easily numbered in rotation (fig. 9), and the series finished off by Braun's method. The numbering is quite definite, and the system clearly presents a "rising phyllotaxis." Thus if the sixth member were over the first, it would be $\frac{2}{5}$, but it is not; nor does 9 come opposite 1, nor again 14, though 22 is so near, that taking all the leaves in sight as in *Sempervivum*, it might be considered sufficiently accurate. If the series has stopped at any one of these points and remained constant afterwards, the transition

* Henceforward, therefore, the term *phyllotaxis* will be used exclusively for the primary arrangement of lateral members at the moment of their actual development on the growing-apex. Schwendener, following the custom of systematists, uses the term as applicable to any leaf arrangement at any part of the plant, as calculated, that is to say, by the very questionable method of orthostichies. Thus the terminal bud of *Pinus sylvestris* would present scale-leaves and spur-branch origins with a divergence of $\frac{21}{55}$, while in the shoot immediately below the divergence was $\frac{5}{13}$. It is clear that the arrangement at the growing-point is the feature of primary importance ; subsequent alterations are secondary in character, and the actual arrangement observed in adult members may present merely the obscured relics of a primary construction ; the hypothesis that the phenomena observed on an adult member has been from the first the aim of the organism having no satisfactory basis.

from one cycle to the next would have been clear. In this actual specimen the ultimate stage reached, as shown by the parastichies of the disk-florets, would have been $\frac{55}{144}$ (cp. fig. 53): the scales, however, pass on to this from the low divergence of the axis with absolutely no visible line of demarcation between ascending members of the series. That is to say, there is no visible "*prosenthesis*" anywhere; the spiral, as in *Sempervivum*, can be given any fractional quality according to the point at which the observer or the specimen stops. In fact, just as orthostichies cannot be proved, so prosenthesis is a purely idealistic conception ; the angles subtending the scales pass on by imperceptible gradations, so that, whichever scale be numbered 1 as starting point, no difference in the construction can be observed.

Clearly, then, there is only one uniform genetic spiral as indicated by the numerical order of development, and no manipulation of phyllotaxis-fractions will explain the system: as pointed out by Bravais,* the error of observation is such that it is impossible to *disprove* that the angle is not constant for every member, and might in fact be the "ideal angle" throughout.

From the preceding example of *Euphorbia*, the conclusion was reached that phyllotaxis is a function of the first zone of growth in which no elongation takes place beyond the equal growth of all the isodiametric initial-cells isodiametrically.

All further investigations, therefore, demand *the elimination of the secondary elongation of the second zone of growth*, either by looking vertically down on the growing point, or by resolving all forces into their transverse components.   The following example of a type in which this elimination of the longitudinal extension has been combined with transverse extension on a large scale may be considered.

5. Phyllotaxis of Helianthus annuus, *L.*

The most perfect examples of phyllotaxis easily obtainable are afforded by the common sunflower, so frequently selected as a typical

---

* *Loc. cit.*, p. 71.

PLATE V.

Fig. 10.—*H. lianthus annuus*, L. Capitulum in fruit,
3 inches diameter; contact parastichies (34 + 55).
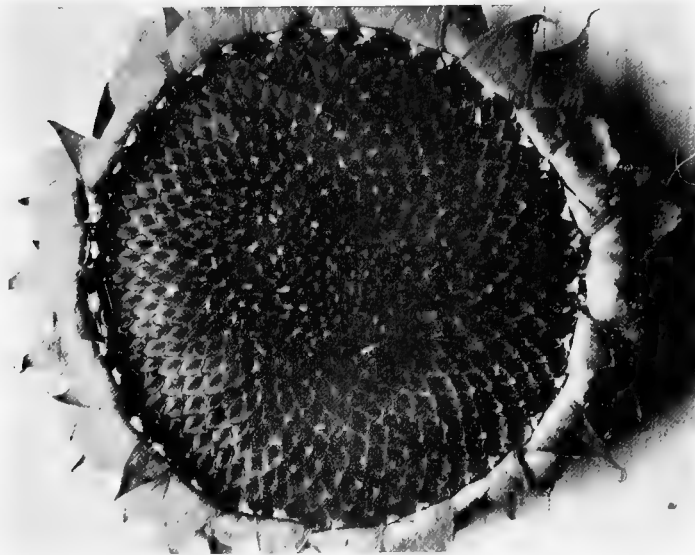
Fig. 11.—*Helianthus annuus*. Empty receptacle (34 + 55);
the ovary portions of 35 abortive ray-florets persist.

Angiosperm, both in anatomical and physiological observations, owing to the fact that it exhibits, par excellence, what is regarded as a normal structure little modified by specialization for any peculiar environment.

Not only is *Helianthus* a leading type of the Compositae which hold the highest position among Angiosperm families, but amongst this family it flourishes in the best stations, in which sunlight, air and water-supply are perhaps at an optimum for modern vegetation. The very fact that it is as near an approximation to the typical Angiosperm as can perhaps be obtained, suggest that the phenomena of growth exhibited by it will also be normal, and from the time of Braun to that of Schwendener it has afforded a classical example of spiral phyllotaxis.

As is well known, the plant forms a main axis of only annual duration, growing 7–8 feet, or in special cases even 15 feet, during the summer months; the leaves are typical in character, and are borne spirally with a divergence to which, since the stem has passed through a very active zone of elongation, the application of any fractional value must be purely empirical, but it would be generally said to range between $\frac{2}{5}$ and $\frac{5}{13}$. In the open, the stem grows erect without torsion, and terminates in the main inflorescence. Branches are normally developed to the second degree, and these again terminate in inflorescences similar to the terminal one, but on a progressively smaller scale. The vegetative leaves pass gradually by reduction into an involucre of leaf-base scales (fig. 14); and contemporaneously with the formation of these, the axis broadens out, elongation practically ceases, but lateral extension is very considerable, so that the capitulum disk approaches a level surface and the whole energy of growth is directed radially.

As in *Cynara Scolymus*, the involucral scales exhibit therefore the phenomenon of a "rising phyllotaxis," and it is futile to attempt to give it any fractional value until the broadest diameter of the inflorescence is reached. Here the leaf-members become fertile scaly bracts and subtend the florets of the disk; the sterilized ray-florets being subtended by the innermost series of the large scales. The fertile bracts mark out rhomboidal areas and the enclosed flower-primordia are circular in section:

bracts and subtended flowers are developed centripetally (*i.e.*, in normal series), and by a wonderful correlation of growth in the whole capitulum, the receptacle extends laterally and symmetrically as new flowers are added, expand, and pass on into the fruiting condition. The result is that the head in fruit exhibits practically the same structure as in its early stages, but on a large discoid area.

Such capitula admit of ready observation. By taking a head in which the last flowers are withering, and clearing away the corolla tubes, the developing ovaries are seen to mark out rhomboidal facets (fig. 10), and when the fruits are ripened and have been shed, the subtending bracts still form rhomboidal sockets (fig. 11).

These sockets, with or without fruits, form series of intersecting curves ("parastichies" of Braun, "contact-lines" of Schwendener), identical with those of the Pine cone, only reduced to a horizontal plane.

A fairly large head, 5–6 inches in diameter in the fruiting condition, will show exactly 55 long curves crossing 89 shorter ones (fig. 12). A head slightly smaller, 3–5 inches across the disk, exactly 34 long and 55 short (figs. 10, 11); very large 11 inch heads give 89 long and 144 short (fig. 13): the smallest tertiary heads reduce to $21+34$, and ultimately $13+21$ may be found; but these being developed late in the season are frequently distorted and do not set fruit well.*

A record head grown at Oxford in 1899 measured 22 inches in diameter, and, though it was not counted, there is every reason to believe that its parastichies belonged to a still higher series $(144+233)$. The Sunflower is thus limited in its inflorescence to certain set patterns (according to the strength of the inflorescence axis,) *e.g.*, $\frac{13}{21}, \frac{21}{34}, \frac{34}{55}, \frac{55}{89}, \frac{89}{144}$. These were first observed by Braun,† and translated into terms of the Schimper-Braun series they would correspond to divergences of $\frac{13}{34}, \frac{21}{55}, \frac{34}{89}, \frac{55}{144}$, and $\frac{89}{233}$ respectively.

---

* *Cf.* A. Weisse : "Die Zahl der Randblüthen an Compositenkopfchen in ihrer Beziehung zur Blattstellung und Ernährung (*Pring. Jahrb.*, xxx. 453). Complete data for 140 specimens are tabulated ; out of 61 poorly nourished pot-cultures 27 produced $(13+21)$ terminal capitula.

† *Flora*, 1835, p. 157.

PLATE VI.
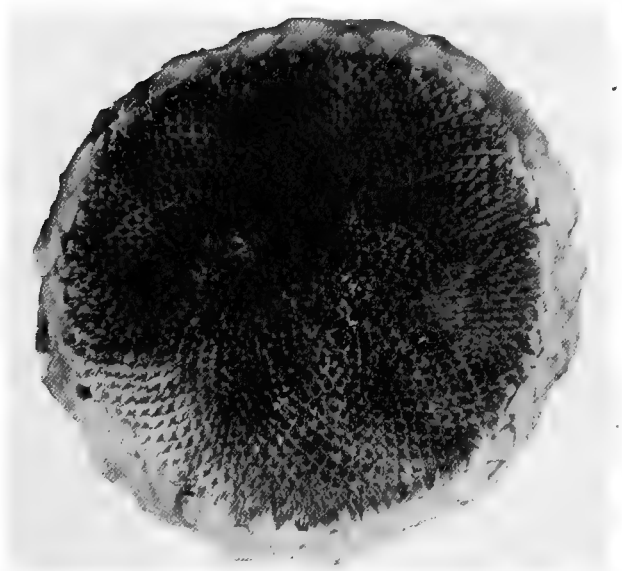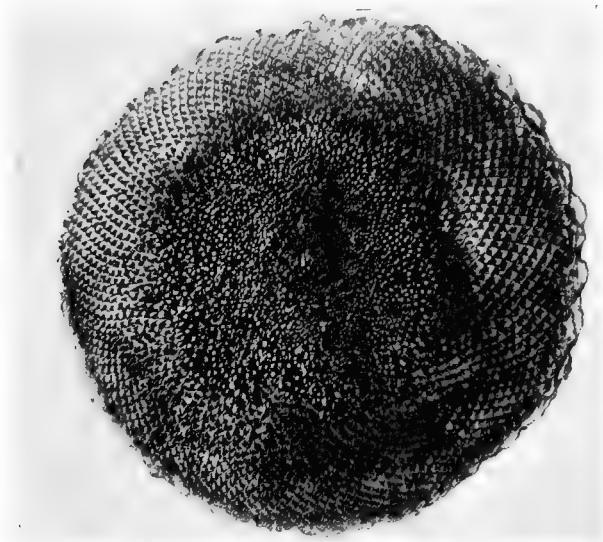
FIG. 13.— *H. lianthus annuus.* Disk 11 inches diameter; contact-parastichies (89 + 144).

FIG. 12.— *H. lianthus annuus.* Disk 5½ inches diameter; contact-parastichies (55 + 89).

Under normal circumstances of growth, the ratio of the curves is practically constant,* and in noting the wonderful accuracy with which these high divergences are illustrated, one naturally concludes that laws which hold with such mathematical exactness in the higher series must also be true when lower divergences are considered. Such an apparent confirmation of the Schimper-Braun theory is very striking; in fact, its very perfection leads one to question the accuracy of the spiral hypothesis; if a single growth spiral can here work at an angle correct to minutes and seconds, and the difference between $\frac{34}{89}$ and $\frac{55}{144}$ is only $1'$ $41''$, why is the mathematical precision not equal in simple cases, and the divergence as readily measured as the angles of a crystal ? †

* *Cf.* Weisse. Out of 140 plants 6 only were anomalous, the error being thus only 4 per cent.

† A primordium of the highest system described (*Helianthus* capitulum, fig. 13) subtends an angle of only $2° 5'$.

On the other hand the range of error in lower systems is very considerable. As an example a seedling of *Nymphaea alba* may be taken, since the leaves arise perfectly free from one another. There are thus no lateral pressures in the bud ; the interstices are packed with hairs among which the leaf bases slide without meeting any resistance (fig. 94).

By making a careful camera-lucida drawing of such a plant 3 mm. in diameter, magnified 70 diameters, restored to normal volume as far as possible by clearing in Eau de Javelle, the centre of the vascular bundles may be taken as representing the centre of construction and the angular divergence measured on the drawing with a considerable amount of accuracy. In such a specimen the angles measured were—

Between 1 and 2	.	.	.	.	.	$147°$	
,, 2 ,, 3	.	.	.	.	.	$126°$	average $139°$
,, 3 ,, 4	.	.	.	.	.	$144°$	
,, 4 ,, 5	.	.	.	.		$143°$	
,, 5 ,, 6	.		.		.	$134°$	average $140\frac{1}{3}°$
,, 6 ,, 7	.	.	.	.		$144°$	(Fig. 94.)

Three leaves form a complete cycle, and the error of observation diminishes in taking the average of the three ; while the centre of each leaf may be fairly accurately marked, the actual centre of the system is difficult to judge on an apex which is bulging asymmetrically.

Thus on another apex (fig. 94, corner) an obvious error of $\frac{1}{2}$ mm. in judging the centre thus empirically, introduced in the divergence of two particular leaves, an error of $143°$ to $147°$; the angle to the next leaf not so much affected by this error being $133°$ or $132°$. In the Schimper-Braun system, the phyllotaxis of

Further observation shows again that while as in *Pinus* and *Euphorbia Wulfenii*, a formula may be obtained from the curves, no obvious orthostichies are present, and the genetic spiral cannot be traced without numbering the members.   An alternative hypothesis thus immediately presents itself, as in preceding cases, namely, that the single genetic spiral of Schimper is not a primary cause of the formation of parastichies, but that the parastichies are the primary, as they are the only constant feature; and that the genetic spiral is of no real significance, but an appearance produced on elongated axes by pulling out such a system as that here found in an arrested condition.

Further examination of the head brings out the interesting detail that the sterile ray-florets are closely related to the long curves, and typically equal to them in number, while their three-angled ovaries form the " half-bricks " which fill out the mosaic of the disk to the circular outline of the involucre (fig. 11).*

Other Composites, especially those with bracteate inflorescence receptacles, are equally constant, though in usually lower series; good examples being afforded by *Aster*, *Chrysanthemum*, and the monstrous forms of florists' Dahlias (fig. 16).

To sum up, the fruit-heads of the Sunflower present a persistent phyllotaxis system in which the members still retain, as in the Pine cone, the actual lateral contact they had when they were formed, unmodified by longitudinal extension.   Growth has operated so symmetrically that the structure of the capitulum is practically the same as when the flowers were being first laid down on the apical cone.   That such is the case may be readily checked by transverse sections of the young inflorescence, in which the circular outline of the flower primordia is clearly defined.   The primary members, it is true, are reduced to supporting frameworks enclosing cylindrical florets; but allowing for this peculiarity, the Sunflower-head presents on a large scale the actual conditions

this seedling would be described as $\frac{2}{5}$, or 144° angular divergence.   According to the theory subsequently put forward, the angular divergence of the system approximates 138°·5, as measured on a geometrical construction.

* *Cf.* Weisse, *loc. cit.*   Ludwig, *Bot. Centralb.*, lxiv. p. 100 : " Ueber Variationskurven und Variations flächen der Pflanzen."

PLATE VII.
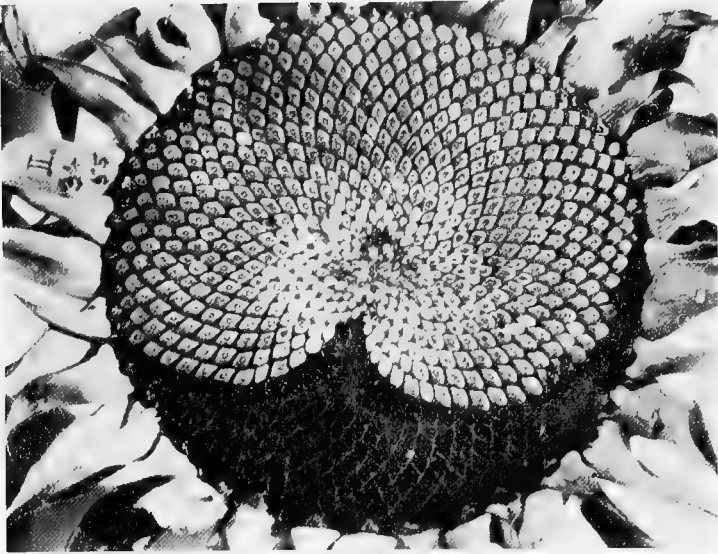
FIG. 15.—*Helianthus annuus.* Capitulum selected as a type. Contact-parastichies $(34 + 55)$; fruits partially removed to show the direction of the curves.

FIG. 14.—*Helianthus annuus.* Terminal bud with developing capitulum.

PLATE VIII.
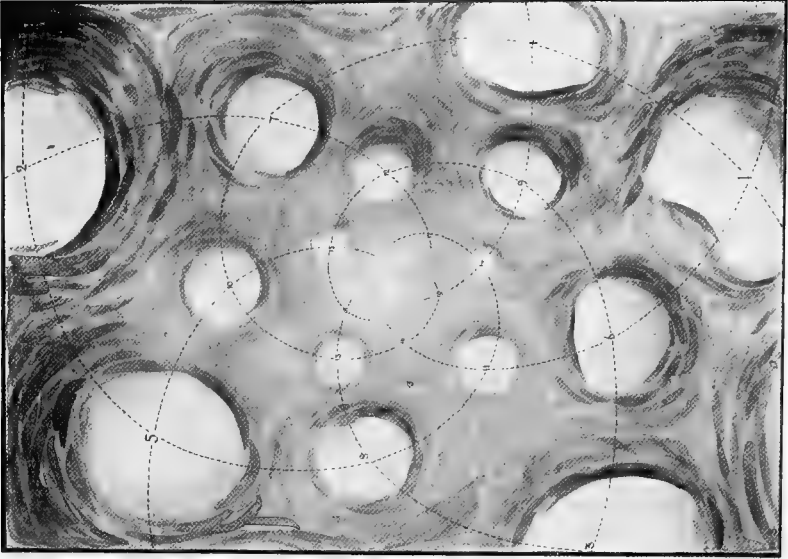
Fig. 35.—*Aspidium Filix Mas.* Growing point of rhizome
(3 + 5) system. Cam. Lu'id. drawing of the whole apex
of the plant as seen in January.
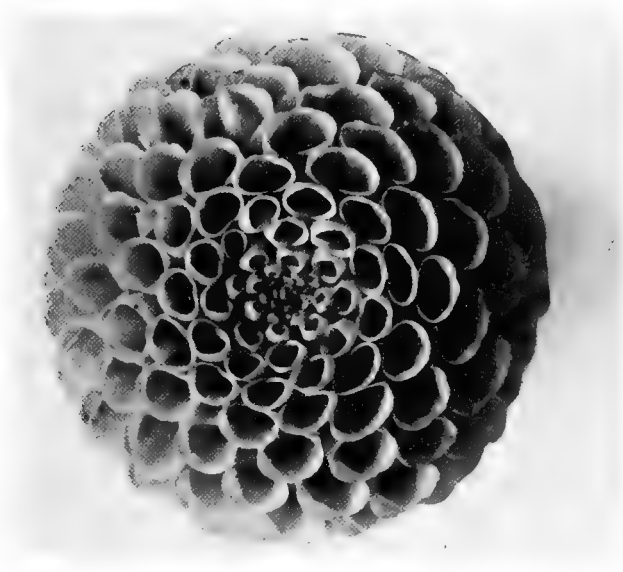
Fig. 16.— *Dahlia.* Garden monstrous form; parastichies
(8 + 13).

obtaining in a transverse plane at the growing apex of a stem, and the whole forms a striking image of a growing point covered with primordia which tend to assume the form of spheres.

It will be further noted that the structure cannot be defined in terms of the Schimper-Braun theory. As in the case of the Pine cone, no formula can be given for it except that which includes the number of intersecting parastichies. But on the other hand, the older theory gave a method for constructing the diagram, which, even if erroneous, was almost within the limit of the error of observation. Clearly no advantage is to be gained by throwing away the Schimper-Braun construction until it can be replaced by a better. If the number of curved parastichies gives the only strictly accurate account of the system, it becomes necessary to examine these curves and see if they can be brought into line with mathematical terminology and geometrical methods of construction.

III. Geometrical Representation of Growth.

STRUCTURE OF THE FIRST ZONE OF GROWTH.

IF spiral phyllotaxis is thus reducible to a function of the first zone of growth, and is, for example, wholly independent of the circumnutation spiral which is a function of the second zone of growth,* often exhibited most clearly in stems with a symmetrical arrangement of leaves, it is necessary before deducing constructions for phyllotaxis to determine as far as possible the various agencies in operation in the former zone.

The conception of the first zone of growth, as elaborated by Sachs,

---

* The same observation applies to the theory proposed by Airy (*Proceedings of the Royal Society*, vol. xxii., 1874, p. 297, 307), in which a strong condensing force was supposed to act with a telescoping effect on a simple whorled series with a tendency to lateral displacement! Such a condensing force, considered possible as a phenomenon of arrested development of the axis, would be clearly a property of the second zone, and though it may come under the head of secondary changes, will have no influence whatever on the actual origin of the new centres of growth in Zone I.

Schwendener's theory (*Mechanische Theorie der Blattstellungen*, 1878) of a vertical compressing force resembles in many points that of Airy ; his pressure is again derived from the mutual contact of the primordia at their bases *after* they are formed. But such alterations, again, must obviously belong to the second zone of growth, and will, if the pressures are unequal, induce packing of the primordia in close hexagonal series.

Lastly, it may not be amiss to point out that the correspondence of vascular bundles (Bonnet), the shape of the pith (Palisot de Beauvais, 1812), or the presence of ridges on the stem (Naumann), being phenomena originated in the third zone of differentiation, have still less importance as indicating any relation whatever to the actual arrangement of the new centres of growth in the embryonic protoplasm of Zone I.

includes an apical region in which the embryonic protoplasm is engaged in the formation of new cell-units, without regard to any marked longitudinal extension of the member as a whole, and may be taken to imply the general increase of the protoplasmic mass, equally in all directions in space, and uniformly throughout its substance; the actual subdivision into units of an approximately equal size being a secondary specialization.   The mass of protoplasm may be thus considered as a whole, without reference to the cell-membranes of the component units, and this in its structure, and in being supplied with new material along an axial-conducting portion, presents many analogies with a jet of semi-fluid substance.

Sachs * also pointed out the remarkable similarity of the shape of the growing apex of a plant to a paraboloid of revolution, and that in a radial longitudinal section of a typical apex the periclinal walls formed a series of confocal parabolas crossed by a coaxial system of confocal parabolas which formed the anticlinal walls.   The mathematical fact that two such sets of confocal parabolas intersect at all points orthogonally was of the utmost importance in enabling him to formulate his theory of the orthogonal intersection of cell-walls.   Sachs, however, left the matter entirely a theory of geometrical construction, although, as he himself states in deciding against the spiral theory, geometrical constructions tell nothing of causes but only express facts; still it is clear that these phenomena must be based on some definite laws, probably mechanical.

Thus Errera † has shown that the cell-wall at the moment of its formation has the properties of a weightless fluid film, and that the direction taken by such cell-membranes is identical with that taken by soap-bubble films which impinge orthogonally on previously-formed films.   A large number of cases proposed as presenting an apparent contradiction of Sachs' generalization have been shown

* Sachs, *Lectures on the Physiology of Plants*, Eng. trans., 1887, p. 448 : " Many hundreds of median longitudinal sections through growing points of shoots and roots, drawn by very different observers without even the most distant perception of the fundamental principle, accord with the construction I have given, *and demonstrate its accuracy*."

† Errera, " Ueber Zellenformen und Seifenblasen," *Biol. Centralb.*, 1887, 1888, p. 728.

by Wildeman * to really support it, so far, that is to say, as an angle of 90° can be judged by the eye in a cleared preparation; and the law of the orthogonal intersection of cell-walls at a growing apex may be taken as generally accepted.

The most remarkable deduction from this theory of orthogonal cell-formation is that the cells at the initial group in Zone I. are laid down in accordance with definite mechanical laws, and not as the expression of any *aim* on the part of the protoplasm as to their ultimate use in the plant economy. The fact that hexagonal packing appears to be the more frequent case in mature organs is therefore due to secondary alterations in the arrangement, and is the expression, that is to say, of secondary forces initiated away from the growing point itself. In other words, plants form their cells fairly isodiametric and orthogonal in Zone I.; in the second zone elongation and further orthogonal division takes place; while a third zone of differentiation is necessary to correct the errors of Zone I. and convert the mechanically produced cells into units more suited for the performance of their special functions. The unequal tensions set up in this process may result in the rolling of the cells over each other as they tend to round off and become more independent.

On the other hand, it is quite true that the orthogonal position is very difficult to prove absolutely in any particular cell. Angles may look very like right angles without being exactly 90°; for example, it is often difficult in a transverse section of the apical cell of *Pteris* to say whether the curvilinear angles are 90° or nearer 120°. It is, in fact, only by bringing the great mass of facts into line with some general mechanical principle, as Errera has done, that the probability becomes practical proof.

Thus when the large oospheres of *Fucus* or the tetráspores of one of the Florideae are discharged, they assume an apparently perfectly spherical form, although this is not the shape in which they are actually developed. But regarded as masses of a dense fluid freely suspended in a non-miscible medium of approximately equal density, the surface tension is sufficient to reduce their surface to a minimum, and spherical form is attained by these reproductive

* Wildeman, *Études sur l'attache des cloisons cellulaires*, 1893.

cells which are not exhibiting any phenomena of growth.   The sur-
face tension is sufficiently great to warrant the neglect of the weight
of the mass of the spore, which would tend to destroy the spherical
form if the densities were slightly unequal ; thus so far as observa-
tions can go, the spores are absolutely spherical ; but no proof of
this exists unless the mechanical theory of surface tension can be
applied.   *That is to say, the absolute proof of the shape assumed can
only be determined by physical deductions and not simply by observation.*

In the same way, no amount of actual measurement of a specimen
would convince a mathematician that the apparently parabolic
curves seen in sections were of the strict ($y^2 = 4\,ax$) type, unless
some mechanical determining cause can be adduced in support of
such a statement ; as, for example, a hypothesis that the cells might
be regarded as homologous with projectiles discharged from the
growing apex.

The paraboloid theory of Sachs still remains a good working
hypothesis, and will stand or fall as the theories based on it can or
cannot explain other allied phenomena ; its value depends on the
extent to which other facts can be deduced from it.

Thus, if the section of the growing apex is a true parabola, over
which the superficial cells may be supposed to glide until they reach
a position of rest on the cylindrical surface of the full-grown stem,
it is possible that the motion in the particles composing the fluid
mass of protoplasm might be resolved into a transverse *velocity* and
a longitudinal acceleration ; the former, a steady uniform movement
due apparently to the expansion of growth ; the latter, the expression
of the constant action of some retarding force acting along the axis
of the paraboloid apex.

In a simple case in which none of the particles were discharged
above the horizontal line, it is clear that a paraboloid of revolution
would mark out the enclosing curve of the line of fall of all of
them ; while if the particles are regarded as being discharged in all
directions, as in the fall of particles of a bursting shell, the
enveloping curve would still be such a paraboloid, so that it is
immaterial whether the initial point be regarded as situated on the
surface of the apex, or at the focus of the parabola, so far as the
main outline of the curve is alone concerned.

C

But there is no reason to believe that growth can be expressed as a uniform velocity, nor can the retarding force be in any way measured, so that the parabola cannot be at present constructed from physical data. This geometrical construction therefore remains purely hypothetical; and although the approximation may appear close to the eye, it cannot be used as a basis on which a mechanical theory of the apex can be built.

From the apparent paraboloidal shape, Sachs deduced the orthogonal intersection of cell walls. The latter may, however, still be true and yet the curves not be parabolas; the law of the orthogonal distribution of paths of equal action being a generalization of which intersecting confocal parobolas is only one special case.*

* The theory of the orthogonal intersection of cell walls, built up by Sachs and Schwendener, was elaborated by the former in one of the most suggestive chapters of his *Vegetable Physiology* (Eng. trans., 1887, p. 431). Plants exhibiting circular symmetry presented radial anticlinals intersecting circular periclinals; in elliptical forms, the periclinal ellipses were intersected by hyperbolic anticlinals, and in the growing apex two orthogonally intersecting systems of confocal parabolas were assumed; again, in the asymmetrical growth of a tree-trunk (p. 445), a diagram constructed by eccentric circle systems showed that the medullary rays followed approximately the paths of radiating orthogonally intersecting curves. The completeness of the generalization is somewhat marred by the consideration that the most remarkable feature of all would be the fact that the plant body, out of the infinite variety of curves, should be so prone to express its form in terms of conic sections. The fallacy is at once suggested, that such plant-curves only approximate these conics to the eye, merely because the eye may be prejudiced in favour of such comparatively simple curves in that they are the first curves to be studied mathematically. From such doubtful premises, Sachs deduced the law of orthogonal intersection of cell-walls; the latter fact may be perfectly true, and there appears to be in fact so much physical evidence in support of the view that it may be instead taken as the real starting point for determining the nature of the main curve. Thus, if a section is mathematically circular, the anticlinals must be radii, if elliptical they must be hyperbolas, if parabolic the anticlinals must be confocal parabolas in the reverse sense, but it is first necessary to *prove* the circle, ellipse, or parabola, as the case may be. There may be an infinite number of curves which look like these much-studied conics, but it does not follow that they exist in the plant until their mathematical equations can be studied from physical data. Thus Sachs grasped the idea that the construction and segmentation of the plant into layers of cells was only a form of the same general action of forces which produces the thickening deposit of cell-walls and the layering of starch-grains. That the orthogonal construction lines of these

Since the longitudinal section affords no clue, it is therefore necessary to fall back on the transverse components of the growing system.

A transverse section shows a simple concentric circular structure in which cell-walls follow the paths of circles and radii, intersecting therefore orthogonally. That is to say, the circles and radii represent reciprocal paths of equal action, and since the protoplasm is a semi-fluid mass, such paths may be compared to the lines of equal pressure and flow in a plane circular system.

Thus, if fluid films are laid down in connection with radial lines of equal pressure, the periclinal walls will be established, and may be subsequently fixed by a deposit of cellulose. In the same manner, because the anticlinal walls follow the paths of radii, it follows that their position results from another uniform action along the circular paths. These orthogonal paths are interchangeable, and what can be said of one can be inferred of the other. The formation of anticlinal and periclinal walls in such a theoretical apex may be considered therefore as resulting from two motions in the fluid protoplasm, one a radiating current, the other a free circular vortex. Main current movements of protoplasm in the whole growing apex, apart from subsidiary currents in individual cells, may thus be regarded as following along the general lines readily observable in single cells, and known respectively as movements of *Circulation* and *Rotation*. The diagram for the paths of equal action in a transverse section of an apex would be the same as that for the circulation and rotation of protoplasm in an isolated spherical cell, and the mechanical law underlying the geometrical construction of Sachs for the orthogonal formation and intersection of cell-walls would be that such orthogonal paths represent the geometrical consequence of the fact that lines of equal pressure and flow in a fluid medium are mutually at right angles.

bodies might be due to crystallization formed the keystone of the Micellar Theory. With such a standpoint it is the more remarkable that Sachs did not explain the layering of the tree trunk along the lines of an ovoid starch-grain, and did not note that the small end of a typical starch-grain is equally indistinguishable by the eye from a parabola, and presents an equally good imitation of the construction lines of a growing apex.

The same will hold good for the radial longitudinal section, and since lines of equal action are here marked out by orthogonally intersecting cell-membranes, it is possible, though not at all essential, that these curves may be parabolas.

But although in dealing with a semi-fluid protoplasmic mass in which movements are undoubtedly taking place one is tempted to use the terminology of lines of equal pressure and flow, it is clear that no definite movements, implying any considerable transfer of material along any radial or circular paths, can be established throughout the multicellular apex characteristic of vascular plants, or even in the coenocytic apex of the Siphoneae. The same orthogonal paths would in a plane system of electrical conduction mark out lines of equipotential and current flow, the two sets of phenomena being in fact only special cases of the general proposition of the distribution of energy along interchangeable orthogonal paths.

The more ambiguous term, paths of equal "*action*," may therefore be used in preference to any other terminology, although in mapping out such systems the phenomena of the more obvious vortex-motion of a fluid may be used *metaphorically*, and as a term implying a *definite geometrical construction*.

Again, circular symmetry is clearly secondary ; all lower plants, the majority of Algae, Bryophyta, and to a certain extent Vascular Cryptogams, present asymmetrical growth at the apex, due to the fact that new lateral members, in the form of single cells, can only be added one at a time ; this being especially well seen in the growth of filamentous cellular algae.

A transition to a more bulky stage is accompanied by the development of an initial cell cutting off segments in serial lateral order, the three-sided apical cell of the Fucaceae and most Mosses and Ferns being the most typical case.

Primarily, then, it may be said plants possess asymmetrical growth as a necessary consequence of the limitation of new members to serial succession of individual units, and that the symmetrical condition, in which new cells are added at the apex in all directions contemporaneously, is a secondary phenomenon, evolved as a distinct improvement on the older method in correlation with the

more perfect and uniform production of a radially symmetrical axis.

In other words, the "circular-vortex" construction of the symmetrical apex is secondary, and must be regarded as a special case of a more primitive "spiral-vortex" construction, which is not, however, necessarily a peculiar property of protoplasm, as assumed in the original conception of the spiral theory, but the mere expression of asymmetrical growth.

In dealing with the spiral development of lateral members, it is therefore necessary to take as a starting point the more general case of a *Spiral Vortex*, rather than the circular one implied by the typical Angiosperm apex of Sachs.

In such a spiral vortex, the stream lines are *logarithmic* or *equiangular* spirals,* which only reach their pole at infinity, and lines of equal pressure and flow will be marked out by the paths of orthogonally intersecting log. spirals. In other words, each circle becomes a coil of a log. spiral, and the radius is represented by a portion of that log. spiral, which cuts the other orthogonally.

Just as the circular-vortex construction is that of an ideal apex, and is usually masked in any given specimen by secondary phenomena of unequal growth and pressure of the component cells, and possibly even at the theoretically initial group by subsidiary vortices in the main stream, so the spiral vortex structure will also be masked and almost obliterated. Beautiful examples of circular-vortex construction persist in the loose and undifferentiated endocortex of many roots (*cf. Zea, Philodendron*), while a more typical root shows parenchyma more or less hexagonally packed.

The apex of the root of a Fern † affords a convenient example

* The logarithmic spiral is the curve whose polar equation is $r = a^\theta$, where a is constant. It is called logarithmic because another form of the equation is log. $r = \theta$ log. a. The log. spiral has the property that the tangent at any point makes a *constant angle* with the radius vector.

† The tetrahedral cell of the Fern-root is here selected as an illustration, owing to the fact that it is easily observable, fairly large, and in the large apex of a healthy root a considerable number of segments can be obtained in a fairly level series.

At the same time it must be clearly understood that the cell in question cuts off a fourth segment in the sequence to form the root-cap. The exact series is

for the consideration of the spiral vortex plan and the disturbing effect produced by secondary agencies.

As seen in transverse section, the tetrahedral apical-cell cuts off *similar members* in serial order along a right or left-hand spiral, which would clearly go on forming segments to infinity before reaching the centre of the system.

Since by Sachs' theory of cell-formation, and observations on the phenomena of karyokinesis, every cell-segment halves the initial cell, the system represents a type of dichotomy of the apex in which successive segments are distributed throughout a spiral system; and since the volumes of regular tetrahedra are as the cubes of their edges, it follows that the new segment-wall would, if the walls were plane, be formed almost exactly one-fifth * along the side of the initial-cell, and the segments should be very approximately five times as long as wide. Since the walls are curved, and the exact curve unknown, it is not possible to get exact data; but observation and measurement of the segments show that such a ratio is very closely approximated in *Pteris*, as in other

thus broken at every third member in the transverse section. The segments in order are not equally graded and do not form a true log. spiral. This can be actually checked on a careful drawing; the centres of successive segments do not lie on a series of circles in G.P., but a gap is left at every third one. Measurements of the relative length and breath of the segments show the same fact. The general plan of construction is, however, sufficient for an illustration, and for practical purposes the section might be assumed to be that of the apex of the stem of *Equisetum*, which is unsuitable owing to its sharply conical form. The exact shape of the tetrahedral apical-cell of the Fern-root is still doubtful. It is clear that it cannot be contained by four confocal paraboloids of revolution, since these curves would intersect at 120° and not 90°; and all four faces appear identical. Nor can the section be formed by the intersection of three circles at 90°; the figure is obviously dissimilar. It is probable that, at any rate, so long as it is actively dividing, and the asymmetrical construction follows the plan of a spiral vortex, the three walls seen in section must be planes of equal action in such a system, and therefore also as seen in section log. spirals intersecting orthogonally. Such a construction would follow the lines of the diagram more closely than any other.

$$* \text{ Ratio} = \sqrt[3]{2} : \sqrt[3]{2} - 1$$
$$= 1 \cdot 259783 : \cdot 259783$$
$$= 1 \cdot \cdot 206.$$

three-sided apical cells (*Himanthalia*, reproductive shoot); and similarly, successive segments, as they continue to grow, notwithstanding displacements of the segment ends, retain the same ratio very approximately.

The segments cut off from the apical cell, therefore, are very approximately, by actual measurement, similar figures, and conform to the law of uniform growth; the spiral series of such figures is therefore arranged along a log. spiral; that is to say, a line drawn through the centres of construction of the segments would also form a log. spiral; and if the cell-walls were determined only by the lines of equal action in such a system, the cell-area would be most simply mapped out by log. spiral lines, as in fig. 17.

But beyond the progressive increase in the size of the successive members, no trace of the spiral remains in the construction; the apex is committed to the formation of cell-members by a dichotomy from the tetrahedral-cell, formed theoretically by three curved segment-walls intersecting at right angles in an endodernal cell of the parent axis; while no sooner are the segments cut off than other forces come into play;—each cell by its own individual growth would tend to round off and become a sphere, but is prevented from doing so by being in close contact with adjacent members; each younger segment, again, is capable of becoming turgid at the expense of an older one, and thus the apical cell retains all its walls convex outwards, and each segment bulges out so that it is broadest in the middle; further, the orthogonal intersections of the segment-walls, fairly obvious in segments 1, 2, 3 (fig. 18), forming angles of 90°, 90°, and 180°, are rapidly pulled into the symmetrical position, 120°, 120°, and 120°, as in segments 4, 5, 6; the orthogonal segments thus early become irregularly hexagonal; while in the case of such members—and the transverse section shows only twelve segments or four complete coils—it becomes impossible to tell by observation whether the symmetry has not become perfectly circular (fig. 18). In the similar case of the stem of *Equisetum*, this secondary assumption of circular symmetry is indicated by the formation of a whorl of leaves from each cycle of three segments. Continued formation of cell-membranes takes place orthogonally within the primary segments, without reference to the original spiral, and

thus five-sided cells are produced at the ends of the segments, which on further orthogonal division render the system quite irregular (fig. 18; 8, 9).

Spiral-vortex construction is thus almost entirely masked by secondary phenomena due to—

(1) The shape of the initial cell.
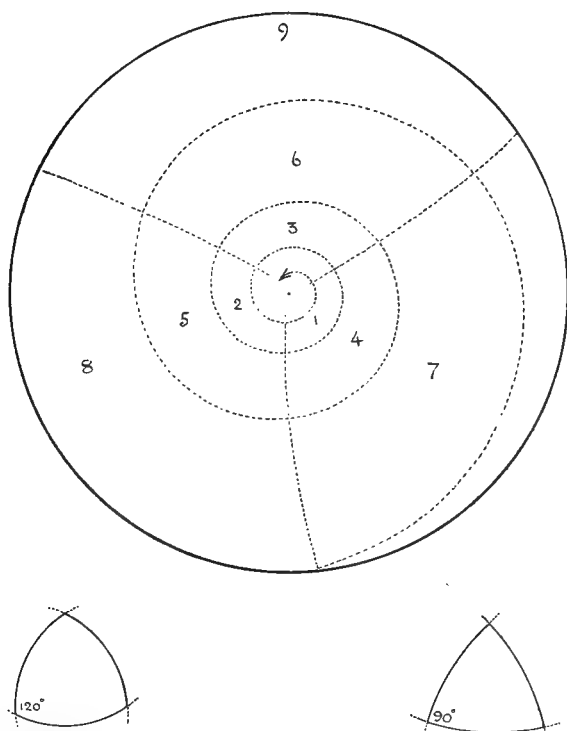
Fig. 17.—Hypothetical log. spiral construction for 3 series of segments at an apex; construction for 3-sided cells by circles intersecting at 120° and 90°.

(2) The effect of the individual growth of the lateral members.

(3) The effects of tensions produced by fused lateral contact.

The effect of dividing up the initial cell into several initials segmenting contemporaneously would be to render the symmetry circular, and the formation of such a system of cell-division proceeding from a single initial in a tissue-mass, in which circular

symmetry is almost immediately attained, may be regarded as a transition from the loose aggregate of lateral members in more simple plant-forms to the symmetrical condition demanded by a radially symmetrical bulky axis.

Now, whatever holds for lateral members of one cell only should also hold for lateral members of cell-aggregates, and the principles of symmetrical and asymmetrical growth in the production of cells in Zone I. should apply equally well to the formation of emergences
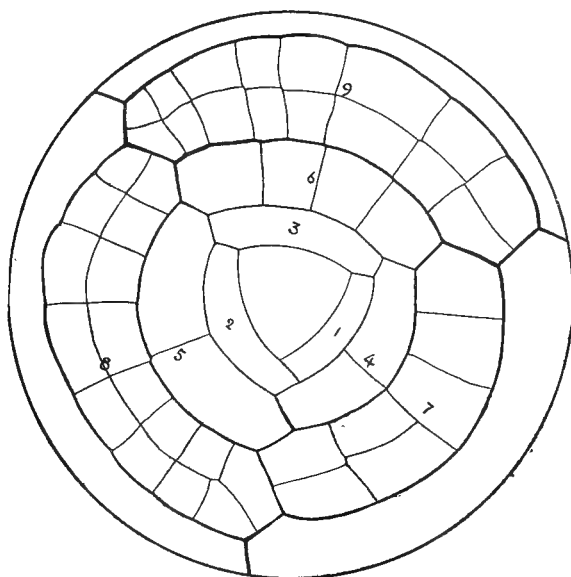
Fig. 18.—Root-apex of *Aspidium Filix-Mas.*

based on these cells, which move over the paraboloid apex in the same manner, but subsequently grow into more massive lateral members, so that the same transition from a primitive spiral-vortex construction to a symmetrical circular one should be traced in the progressive specialization of phyllotaxis.

In the same manner, lateral members would be formed: (1) along paths of equal action ; (2) in a mechanical system, independently of any aim on the part of the plant, with a view to their subsequent functions ; which (3) might require secondary alteration

to suit special requirements; while (4) secondary packing would ensue as a result of unequal growth pressures, and (5) the same tendency towards perfection of symmetrical construction of a radial system would result in the substitution of secondary circular-vortex construction for the primitive spiral system.

Although much of these deductions may appear at first sight fanciful, it is evident that if such generalizations can be successfully applied to the special case of leaf-distribution, the original conception becomes much strengthened. Nor are the hypotheses here put forward more imaginative than that of the paraboloid apex of Sachs which remains incapable of proof, or his construction for the apical cell of *Pteris* which does not satisfy the evidence of his own drawings.

The proposition is then that the genetic spiral is a logarithmic spiral, homologous with the line of current flow in a spiral-vortex; and that in such a system the action of orthogonal forces will be mapped out by other orthogonally intersecting log. spirals,—the "parastichies."

In comparing such a leaf-producing spiral-vortex with that of the cell-producing vortex of *Pteris*, the differences will be due to the absence of the disturbing secondary phenomena. Thus, there is clearly no apical construction to be impressed on the series of members, and the members again are wholly free from one another; they are so far at liberty to assume as far as possible the form of spheres, but when formed in close contact they will exert lateral pressures on each other which, when they cease to be orthogonally distributed, will induce slipping. The theoretical spiral-vortex of phyllotaxis will thus have one disturbing factor only, namely the pressures due to any unequal individual growth of the component members.

GROWTH.

So far, the mass of protoplasm constituting the growing apex has been considered as a constant mass of fluid presenting radiating and circular or spiral-vortex phenomena, as it appears, that is to say, at any given moment of observation.

It is, however, undergoing a constant increase by an expansion throughout the entire mass; and restricting the diagram to the plane circular expression of a transverse section, it is clear that such uniform expansion must be represented by a *circular meshwork of similar figures,* in which any given zone of particles in unit time increases to the next outer zone of the same number of particles of similar character. Such a construction may be represented by a circular network of " squares" formed by the intersection of an indefinite number of concentric circles by a constant number (n) of radii. If "circles" be inscribed in the "square" areas the construction becomes more obvious (fig. 19), since any given "circle" must expand to the one next it on the same radius, which subtends the same angle, and the whole system expands uniformly in all directions. Thus, if two concentric circles are taken infinitely near together, the space between them can be divided into infinitesimal figures, which, even if magnified to finite size, would differ infinitesimally from squares. For small distances, when n is very large they may be regarded therefore as practically squares.

It follows from the construction that the concentric circles are in geometrical progression, while the areas of the similar figures, " squares " or inscribed " circles," are also in geometrical progression along the radial paths.

The law of uniform growth is therefore expressed by a *geometrical* progression and not an arithmetical, and the fact that the parabola of the apex-section cannot be considered compounded of a transverse growth-velocity is so far evident.

Sachs constructed his diagrams on the basis of arithmetical progression, and, regarded from a geometrical standpoint, it is evident that such a construction is correct for mature plant organs. Thus, on comparing the structure of a plane circular plant such as *Coleochaete* (fig. 87) with a theoretical construction, the cell walls are marked out by radii which intersect concentric circles orthogonally, and these latter increase by equal increments from the centre outwards. But a little consideration shows that such construction is not the result of uniform growth, but is the expression of the fact that individual cells attain a certain constant bulk and then stop growing. The plant is thus not continuing to grow throughout its

whole area, but only at the periphery, and the construction by circles in arithmetical progression is therefore the expression of peripheral growth, since if all the cells continued to grow equally, they would form a series in geometrical progression and no new radial walls would be laid down.

The several cases of symmetrical and asymmetrical construction in an apex presenting uniform growth may now be considered in order, commencing with the symmetrical forms, since these present the simplest diagrams.

Restricting the diagram to a plane expression, it is clear that a circular-vortex will be represented by concentric and radial series of similar figures; a spiral-vortex by similar figures arranged along intersecting logarithmic spirals.

If orthogonal figures ("squares") are used in the circular construction, they will also be represented by "square" areas bounded by log. spirals in the spiral-vortex.

The curves ("circles") inscribed in these areas, which approach true circles as the "squares" approach true squares, may be represented by inscribed circles, the difference being within the error of drawing when the angle subtended is small.

IV. Application of Spiral-vortex Construction.

1. Arrangement A.

UNDER this heading may be comprised the simplest construction in which the lateral members are formed in a free circular vortex, and present the appearance known as "*superposed whorls.*" If the members are formed freely on the paraboloid surface of the cone of growth and exert no pressure whatever on each other, they will, if destined to produce radially symmetrical organs, tend to assume the shape of spheres, and may be thus represented by concentric series of circles.

Such a construction is, however, rarely met with; it occurs in flowers (*cf. Primula*), and is in such cases commonly regarded as of secondary origin. Expressed in terms of single *cells*, it occurs frequently in the endocortex of roots (*cf. Zea Mais*), in which the absence of any considerable pressure from the peripheral layers enables the cells to retain the original orthogonal system in which they were developed.

The mechanical construction of the system, again, as expressed geometrically, indicates that if the mutual pressures of the component members are equal for every member, no disturbance of the system can take place. The circles will tend to become squares, this being again well seen in *Zea* root; but no hexagonal packing can be initiated unless some additional force is brought into requisition; such, for example, as may be seen in the *Zea* root, where unequal growth and the pressure of the outer layers induce hexagonal packing in the exocortex when the endocortex may still remain unaffected.
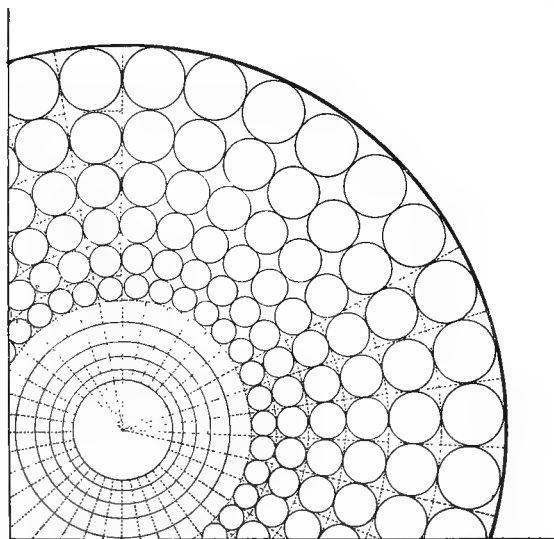
Fig. 19.—Systems of uniform growth : Scheme A ; symmetrical.
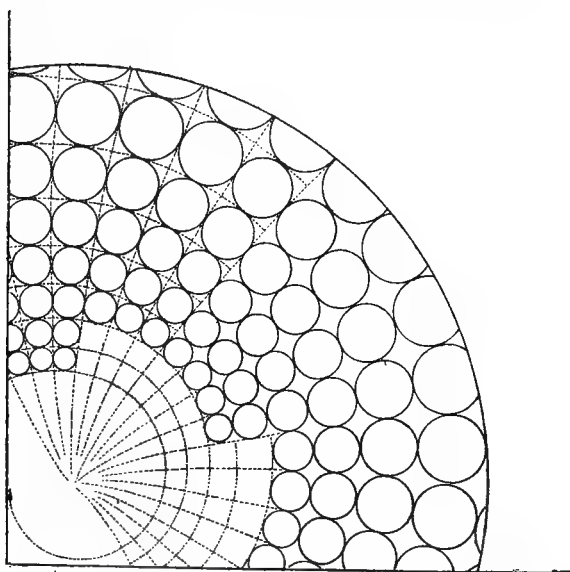
Fig. 20.—Systems of uniform growth : Scheme B ; asymmetrical.

2. Arrangement B.

As previously indicated, the arrangement of superposed whorls in a circular-vortex system can only be regarded as a special case of the more general asymmetrical form of a spiral vortex. In this latter system, therefore, the primordia take the arrangement of "*superposed cycles*."

The circles become log. spirals, and the radii also portions of log. spirals intersecting the former orthogonally.

As the spiral approaches a circle, the difference between the two constructions will be scarcely observable to the eye, if a portion only of the coil is seen; while even when the deflection of the main spiral is considerable, as in fig. 20, where the width of a member is gained in one quarter of a complete revolution, the deflection of the "orthostichy" lines is almost imperceptible to the eye when the construction lines are omitted. This figure thus illustrates very forcibly the standpoint that lines which appear perfectly straight to the eye may still be very definitely spiral, and the orthostichies of Schimper and Braun may have no real basis. On the other hand, a glance at the construction of such a typical phyllotaxis system as that of a capitulum of *Helianthus* is sufficient to show that this type of spiral construction does not obtain in the plant. Nor will any amount of mutual pressure in the primordia produce any change in the system beyond squeezing the spheres into cubes, since they are by construction orthogonally arranged; although it is conceivable that additional external pressures might produce secondary hexagonal packing.

Since, then, such a spiral construction will not meet the requirements of normal phyllotaxis, an alternative method of orthogonal arrangement may be considered.

3. Concentration Systems.

That the primordia at the apex of a growing stem were "condensed" into a confined space, in order that they might be more

securely protected * in the bud, has long been a favourite biological explanation of bud-structure; to the common disregard of the fact that actively dividing cells are capable of sustaining enormous pressures from the surrounding tissues; and that as shown in the apex of *Pteris*, younger cells can grow and remain turgid at the expense of all older ones. The case of pressure against a sclerosed framework may be considered separately, but as far as parenchymatous structures are concerned, there is no reason to suppose that primordia are not strong enough to resist all the pressures that can be brought to bear on them in the bud, and the greatest pressures are of their own making. As already indicated, so long as they are formed in orthogonal series, all such mutual pressures will only tend to alter their *shape* but not their *arrangement*.

From this standpoint of a special packed system, Airy formulated a scheme of phyllotaxis, in which all systems were to be derived from a type presenting a constant "ideal" divergence angle by longitudinal compression. The same idea has been put forward by Schwendener,† and his first figure illustrates the action of a vertical condensing force on a spiral series of the Schimper type, the natural effect of the latter being to change an orthogonal system into a hexagonal one. Without going into further detail as to Schwendener's standpoint, or considering how such a vertical condensing force could be obtained at a plant-apex, the problem may be attacked in a different manner.

If a set of equal spheres be arranged in orthogonal series, all forces of contact will act at right angles to the curved surfaces, in this case circles, and will be represented by the sides of the exscribed square areas. The whole system is in equilibrium.

But since the forces acting along the sides of a square are also represented by the resultant forces along the diagonals, it follows that the same contact pressures will give rise to lines of equal pressure in a secondary orthogonal system. In other words, two methods of arrangement are interchangeable (fig. 21) and equally in equilibrium without any disturbance of the original forces. The diagonal arrangement is equally in equilibrium as is the

* *Cf.* Airy, *Proceedings of the Royal Society*, vol. xxii., 1874, pp. 297–307.

† *Mechanische Theorie der Blattstellungen*, Leipzig, 1878, Taf. 1, figs. 1–4.

vertical one, and the plant is at liberty to choose either construction along two sets of orthogonally acting lines of pressure in the same system.

4. ARRANGEMENT C.

Such an arrangement, the familiar case of "*alternating whorls,*" is, in fact, the one found in the vast majority of symmetrical plant constructions. It presents all the advantages of a "condensed"
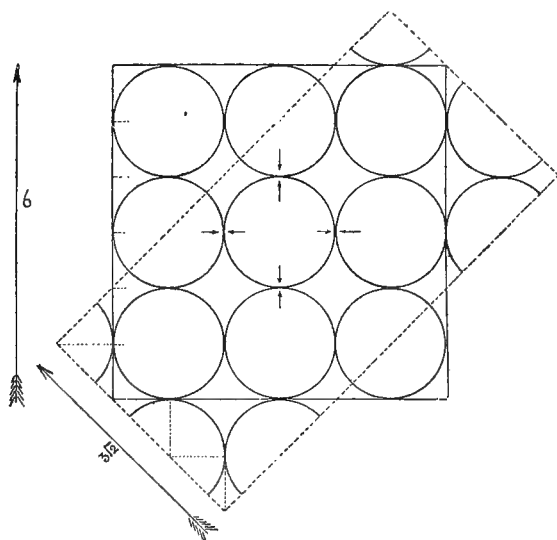
Fig. 21.—" Concentration " system.

system, in that the same number of elements is so arranged that it is shorter longitudinally and broader transversely. The geometrical construction of fig. 21 shows that in such a simple case the shortening of the system will represent a vertical gain of $6 : 3\sqrt{2} :: 2 : \sqrt{2} :: 100 : 70{\cdot}7$, or a gain of up to 30 per cent. as expressed in the number of internodes which can be laid down on a given apex.

Without insisting on any such biological interpretation, as that

D

the plant actually selects such an arrangement in order to secure this gain of concentration, the fact remains that the system is the one found in the vast majority of whorled types, which are again regarded as secondary derivatives from an ancestral asymmetrical condition.

In selecting this alternative whorled construction (fig. 22), note that—

(1) The system remains orthogonal, and is thus equally dependent on lines of equal pressure.

(2) No additional pressure is required beyond those already in action in arrangement A.

(3) However great the growth pressures of the equally developing component primordia, no hexagonal packing will be produced, but the circles will approach square rhombs, unless, as before, growth is unequal, or takes place inside a closed system.

Again, since the whole bulk remains constant, the arrangement is not due to any *condensation*, implying packing, but may be perhaps better expressed by the term *concentration*.

When expressed in the form of a plane circular diagram (fig. 22), the diagonals become orthogonally intersecting log. spirals in that they cross the radii at a constant angle, and a suitable number of these paired spirals will in turn map out the system by their orthogonal intersections, which will give figures which are in the limit squares with inscribed circles.

5. Arrangement D.

The general case of spiral phyllotaxis is now reached by taking the asymmetrical expression of the construction C. The whole system remains orthogonal, but is expressed by a spiral vortex-construction in which the genetic spiral remains as in B the grand log. spiral current line. The radial " orthostichies " will intersect this spiral orthogonally. The two symmetrical log. spirals which mark out the paths along which the members are actually laid down in a concentration system become an asymmetrical pair and form the *Contact-Parastichies* of the system. When the genetic spirals
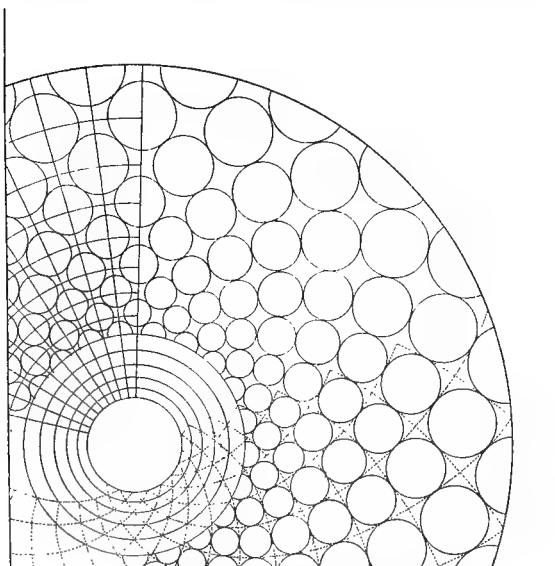
Fig. 22.—Scheme C : symmetrical.
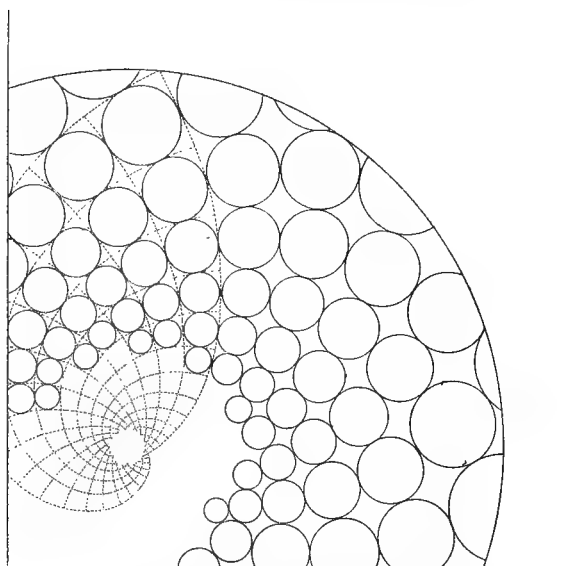
Fig. 23.—Scheme D : asymmetrical.

cannot be traced, and the orthostichies are equally incapable of observation, the whole system is plotted out by taking the observed number of parastichies and expressing them as mutually intersecting log. spirals.

A method is thus attained which gives perfect mathematical expression to such a system as that deduced from observation of the Pine cone or Sunflower capitula, so perfect that any deviations from it in the actual plant must be due to the influence of some extraneous force not yet considered.

The following construction which expresses a $(34+55)$ Sunflower head may be taken as a type :—

Since the whole construction hinges on the diagrammatic representation by intersecting log. spirals, a simple method is required for drawing these curves with a degree of accuracy which will at least cover the error of observation; and, as the graphic constructions will be found to afford sufficient geometrical evidence of the truth of the method, it will not be necessary to include any strict mathematical proof. A simple way of obtaining very accurate results is as follows:—Describe a large circle and divide it into a conveniently large number of parts $(50-100)$; draw the same number of radii through these points, and then, proceeding from the circumference inwards, draw, with the same centre, a series of concentric circles, making with the radii a meshwork of squares, as near as can be judged by the eye. In such a circular network of squares, arranged in radial series in geometrical progression, all lines which are drawn through the points of intersection in any constant manner are logarithmic spirals, and when drawn in reciprocal fashion intersect at all points orthogonally, the simplest case being that in which symmetrical diagonals are drawn across the meshes, which gives, in fact, the preceding case for the structure of alternating whorls (fig. 24).

An *unequal* pair of curves may be selected by taking a diagonal across two squares in one direction on one side, and across two in a converse way on the other; by continuing these, two asymmetrical log. spirals will be obtained having by construction the ratio $1:2$. By filling in such curves all round the figure, it may be proved experimentally that by using the full number of short

curves (1), and half the long curves (2), an asymmetrical network of similar " squares " will be obtained.   To produce these results the number of points into which the original circle was divided must be divisible by two.
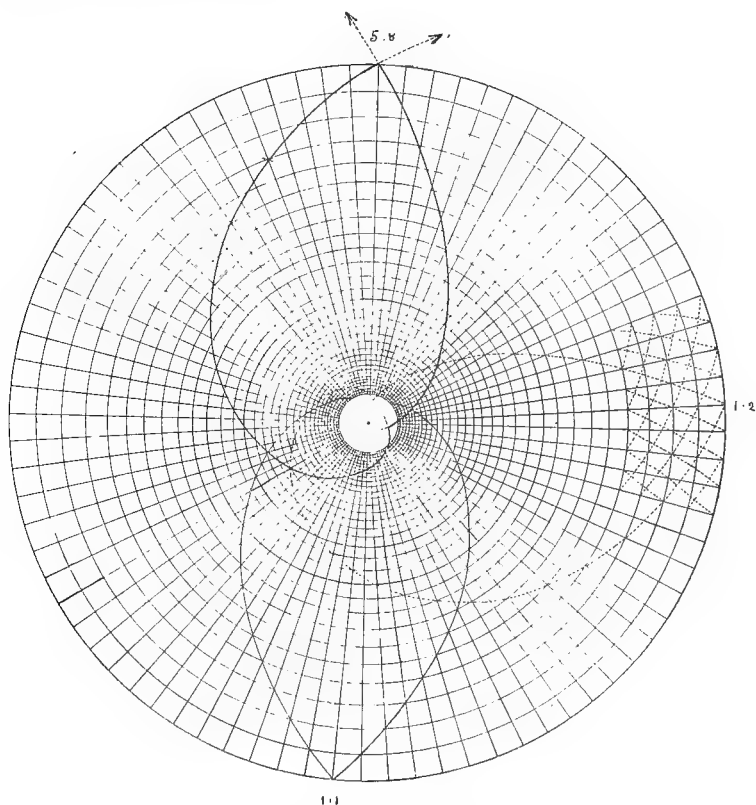
Fig. 24.—Geometrical construction of log. spiral curves :
ratios (1 : 1), (1 : 2), and (5 : 8).

In the same way a pair of curves in the ratio of 34 : 55 may be obtained by dividing the circle into a number of parts, of which 34 and 55 are factors, and drawing two continuous curves across the meshes in the ratio 34 : 55 on one side, and 55 : 34 on the other.   As these numbers are unwieldy, a simple method will

give equally correct results; the ratio 34 : 55 may be taken as 33 : 55 within the error of drawing in small squares, or 3 : 5. The curves (3 : 5), taken in a circle divided into 90 parts, will give results well within the limit of drawing the square meshwork correctly. So close are the ratios of the stages of the continuous

fraction $\dfrac{1}{1 + \dfrac{1}{1 + \text{etc.,}}}$ that within the error of drawing any one will

give satisfactory results; the error being considerable only in the centre of the system, where the difficulty of measuring the squares is also greatest. The true curve for 34 : 55, and in fact that for the ideal angle of the continued fraction, lies between (3 : 5) and (5 : 8), and may be closely approximated from the ratios 3 : 5 in a circle with 90 radii, or 5 : 8 in one of 80.

Such a pair of curves is, then, well within the error of drawing, accurate for a (34 + 55) system, and may be used to map out a spiral orthogonal construction; for practical purposes a pair of curves may be cut out in card, fixed to the paper by a pin through the centre of the circle, and used as a rule. By taking a circle of radius equal to that of the curve pattern, and dividing it into 55 and also into 34 equal parts, so that one point may be common to the two sets, and using the curves as a rule to mark 55 short curves and 34 long ones, the whole circle will be plotted out into a spiral meshwork of squares in orthogonal series, corresponding to the parastichies of the Sunflower capitulum taken as a type, and the plan may now be used as a check on the actual phyllotaxis (fig. 25).

It is obvious that either the points of intersection may be regarded as the centres of construction of the lateral members, or the square areas themselves as the actual members, if packing is so close that no interspaces are left; and the appearance of circular flower - primordia may be indicated by describing 'circles in the approximately square areas. Regarding the point on the circumference common to both sets as No. 1, the whole system may be numbered up by Braun's method, the meshes along the short spirals differing by 55, those along the long by 34.

In such a numbered diàgram, the parastichies $(34 + 55)$ are observed to be by construction a concentrated system complementary to two other curves, the members of which differ by 89 and 21 respectively.
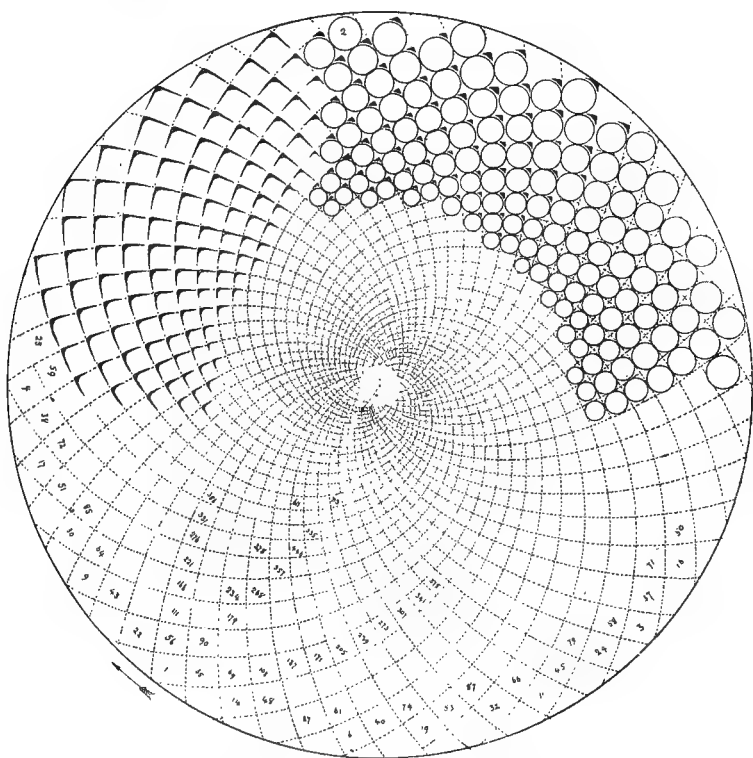
Fig. 25.—Log. spiral construction for capitulum of *Helianthus*, $(34 + 55)$ capitulum taken as a type : genetic spiral winds right.

That the orthogonal system adopted by the plant is the one which makes most nearly for optimum concentration is shown by the comparison of other orthogonal systems which would pass through the same points of intersection. These systems may be deduced from the functions of the summation series of numbers, or taken from the diagram.

Thus taking the parastichies noted, $34 + 55$

and $21 + 89$,

the same points may also (with others) be mapped out by

$$13 + 144,$$
$$\text{or } 8 + 233,$$
$$5 + 377,$$
$$3 + 610,$$
$$2 + 987,$$

and ultimately $1 + 1597$, the least con-
centrated system.

Thus, on reducing the whole system to one grand spiral only,
which is, in fact, the genetic spiral, passing through 1, 2, 3, etc.,
the nearest approach so far to a true orthostichy line is the log.
spiral cutting the genetic spiral orthogonally, which passes through
1 and 1598, a point too near the centre to mark clearly, though
378, 611, 988, are indicated.

The error of attempting to define such a system by the Schimper-
Braun system of fractions, in which it might pass as a $\frac{34}{89}$ type, is
at once apparent: the 89 curve bears no obvious relation to the
genetic spiral, though it bisects the angle between the 34 and 55
curves. The system of intersections may be defined in terms of
any pair of these orthogonally intersecting spirals but not in terms
of one of each of two different sets. The only true expression for
the Sunflower head lies in taking the nearest numerical ratio,
which is that in which the squares, or the circular primordia
contained in them, are in actual lateral contact. There is in the
whole system figured no member radially superposed to number
one, and the construction is thus in agreement with Hofmeister's
law; while other important deductions are—

(1) The genetic spiral follows the direction of the short curves (55).

(2) One coil of the " genetic spiral " approximates a circle, almost
within the error of drawing the system.

(3) The false " orthostichy " line (89) is very nearly a radius, or
within the expression of hypothetical " torsion " in a specimen.

(4) The nearest approach to an orthostichy line (1597) is as
near a radius as the genetic spiral is to a circle.*

* For the true orthostichy line, *cf.* Mathematical notes.

(5) The concentration system adopted is the best possible under the circumstances; and

(6) As indicated by the proximity of the numbers, 34, 55, the *nearest approach to the symmetrical condition*, when such a summation series of constants has to be followed.

In the same manner, making use of the same curve, and dividing the circle into the appropriate number of parts, the other systems for the capitula of *Helianthus* may be plotted out, within the error of drawing, and numbered up with identical results following the geometrical construction; that there are no members radially superposed to form a true " orthostichy " line, so that each one of the constructions naturally fulfils all the demands of Hofmeister's law.   It will be noticed, however, that with a constant direction for the curves, the " genetic spiral " does not run the same way, so that while in fig. 25 (Ps. $= 34 + 55$) the genetic spiral was right-handed, in similar constructions for $(55 + 89)$ and $(21 + 34)$ it will work out left-handed.   Also, the lowest number always gives the number of the longer curves, since in constructions in which the longer curves are formed with the higher numeral the meshes, although orthogonal, are not " squares."

Taking these Sunflower heads alone as matured structures, it appears, then, to be evident that the axes bearing them have impressed on them, at an early stage of their development in the first zone of growth, a certain fixed ratio of curves which follow the lines of equal action in the semi-fluid protoplasmic mass, the transverse components of which may be represented by the construction of a similar number of orthogonally intersecting logarithmic spirals.

The numbers of the curves employed and their ratio appear to be an inherent property of the protoplasm of the plant apex, and may vary from shoot to shoot, but within the same capitulum the phenomena remain constant, except in so far as they may be disturbed by secondary changes due to unequal rates of growth of the members composing the system.

The numbers of the parastichies are the only constants which define the system; since, although the same points of intersection may be plotted out by other related systems of spirals, it can readily be proved by constructing the diagrams that the curves indicated

by the parastichies are the only ones which give these intersections alone, *i.e.*, give the minimum of intersections.

It remains to be considered why such numbers and ratios are found, and to what extent the plant is restricted to such a series.
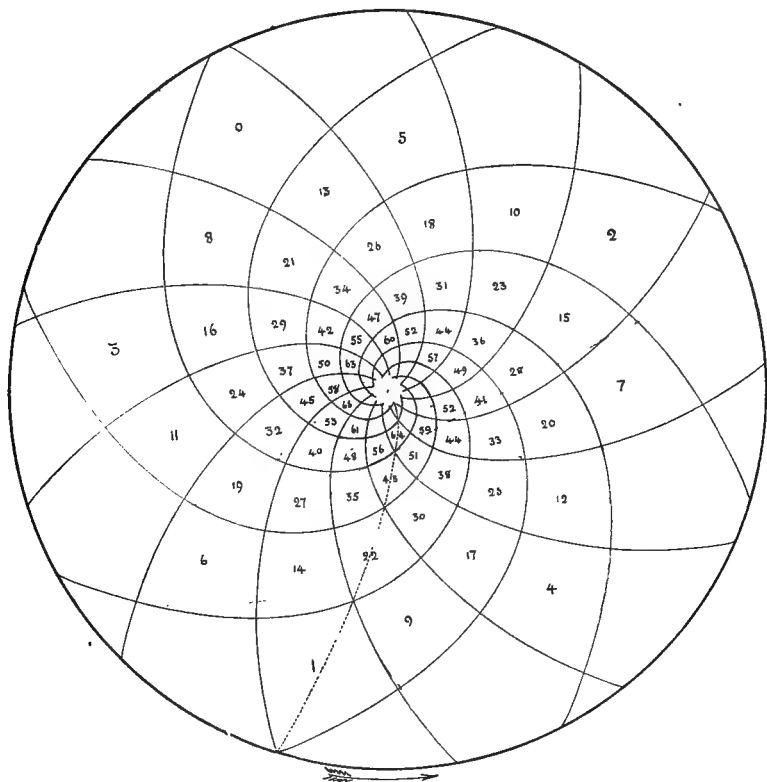
Fig. 26.—Log. spiral construction for system (8 + 13) ; with curve setting of preceding the genetic spiral winds left.

Again, by using the same curve, and drawing eight long and thirteen short spirals, a set of parastichies may be marked out which will give equally correct results for the Pine cone (*P. austriaca, P. Pinea*) ; and, on numbering the areas, they may be checked by the actual specimen : all observed appearances are accurately imitated in the diagram ; the axes of the rhombs of rhombs forming spirals

instead of radii as demanded by the Schimper-Braun theory, while it is clear that any attempt to correct the Schimper construction by demanding hypothetical displacement or torsion in the cone is entirely unnecessary.   The balance of evidence must fall on the side which explains most facts with the least amount of straining.
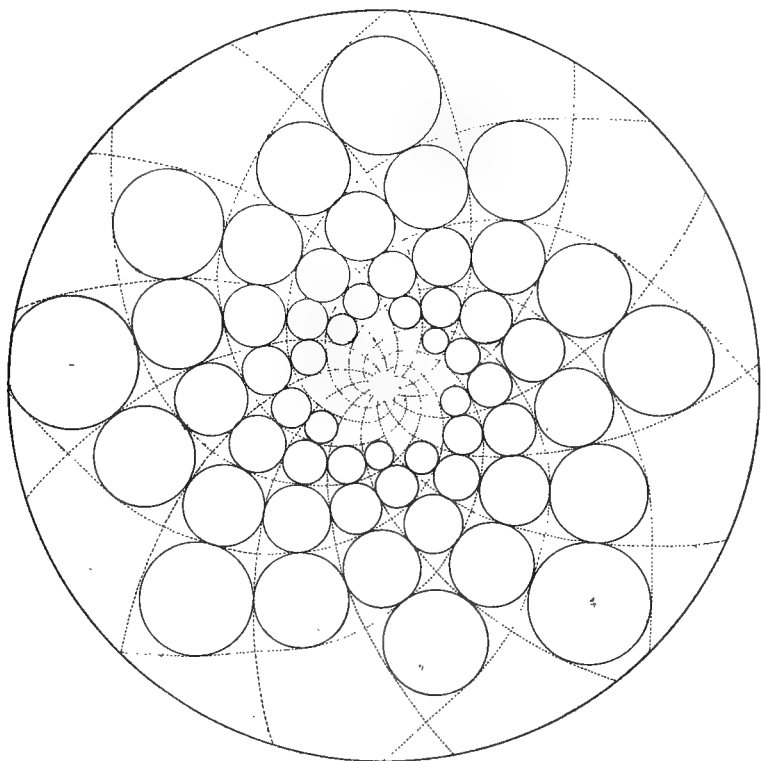
Fig. 27.—The same, with inscribed circles as representatives of the primordia.

By inscribing "circles" in the "square" areas (fig. 27) the diagram may be arranged to fit the case of spherical flower-primordia, as in the inflorescence of *Scabiosa atropurpurea*, in which the bracts are omitted; while it is equally correct for the androecium (8+13) of *Helleborus niger*, or for the bractless

spadix $(8+13)$ of *Anthurium crassinervium*, so widely is this type of construction distributed among flowering plants.

The diagrams are less satisfactory in the lower ratios, owing to the fact that but few members can be represented on a circle, this being correlated with the production of relatively large lateral members over a greater vertical extent of a narrow axis; but they are sufficiently clear to show (1) the approximate alternation of successive cycles, (2) the fact that the first member of each successive cycle falls on a spiral line and that there are no radial orthostichies present. On the other hand, when parastichies are drawn through the points of intersection of radii and circles as demanded by the Schimper-Braun construction, these curves, which irritated Sachs,* are seen to be neither log. spirals nor mutually orthogonal, and the essential points of their construction are lost.†

The series of common phyllotaxis expressions can therefore only be represented in terms of the intersecting contact-parastichies, in the form : Ps. $= (1+1), (1+2), (2+3), (3+5), (5+8), (8+13)$, etc., in which the first number (the lowest of the pair) gives the long

---

* Sachs, *loc. cit.*, pp. 497-498 : " Among the errors of this (Spiral) theory is the one that the spiral arrangement of all organs on a common axis must necessarily follow from its so-called parastichies." " Even ordinary wall-papers show such parastichies, and in the same way the arrangement of scales on the bodies of fishes, of the hairs on the skin of mammals, and of the tiles on a roof, exhibit such parastichies clearly enough."

† Van Tieghem, *Traité de Botanique*, vol. i. p. 63. A construction of a $\frac{2}{5}$ system with the genetic spiral represented as a Spiral of Archimedes gives points along 5 radii vectores which are the orthostichy lines of Schimper. Curves drawn through the points differing by 2 and 3 respectively are again by construction Archimedean spirals in the ratio 2 : 3. Such a simple spiral construction was evidently present in the minds of Bonnet and Calandrini in proposing the original quincuncial system, and the fact that they observed that leaves did not obey such a construction accurately was thus glossed over as a secondary biological phenomenon. Similarly all the divergence fractions of Schimper and Braun clearly imply constructions by Spirals of Archimedes, and these spiral systems are thus based on the fact that orthostichies are often fairly accurate to the eye.

The Archimedean spirals, it is important to note, are based on hypothecated orthostichies, and not the orthostichies on postulated Spirals of Archimedes. Since, then, these spirals are usually associated with torsion phenomena and the formation of screws, various torsion-hypotheses become superimposed on the original unproven premises.

curves, and the ratio of the numbers indicates the degree of asymmetry of the system.

Any attempt to express a fractional ratio leads to misconception of the phenomena.   Such a construction, however, can only be applied to a system in which it is still possible to observe the
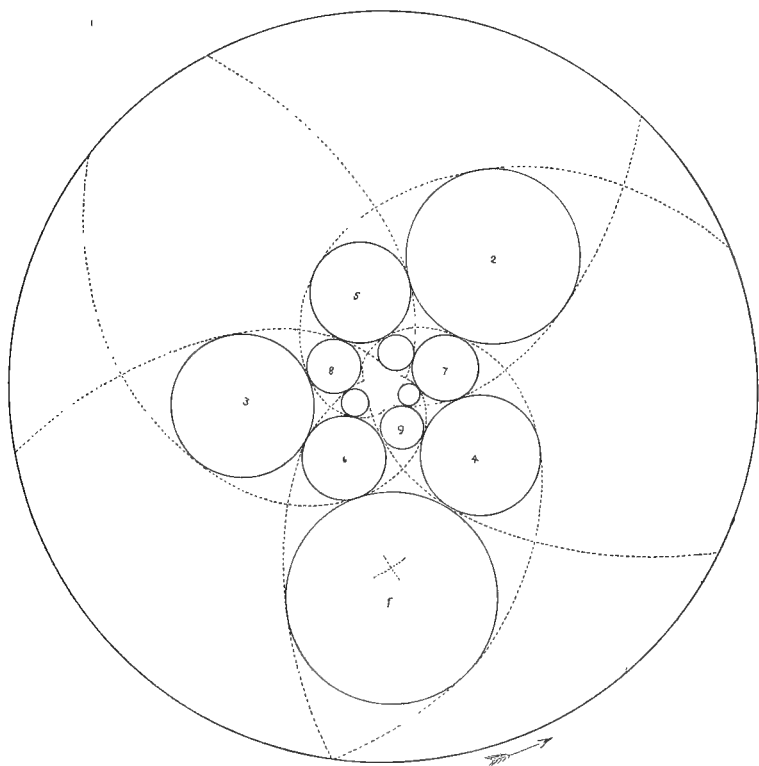
Fig. 28.—Log. spiral construction (3 + 5).

actual curves of contact, either on the mature plant or in the bud; the Schimper system may still remain a plausible account of the mature leafy axis, which has passed through a possibly uneven zone of elongation, since it certainly supplies a demand ; and, so long as it is remembered that it is only an approximation, no great harm will be done, and it will continue to be as useful as in the past.

6. HELICES AND SPIRALS OF ARCHIMEDES.

Mature cylindrical axes exhibiting spiral phyllotaxis in which the lateral members are closely set and of uniform character, present remarkably beautiful appearances of helices with parallel screw-threads winding in converse directions (*cf.* figs. *Stangeria*, (29), *Cereus* (30), *Euphorbia* (31), *Araucaria* (32).).

Such spirals with equidistant coils continued upwards on a cone, would on the unrolled surface constitute portions of Archimedean spirals as pointed out by the Bravais, and the projection on a transverse plane would similarly give intersecting Archimedean spirals.

The fact that similar helices are produced by torsion action apparently forms the basis of all torsion theories of phyllotaxis, whether in the obvious form of Airy's hypothesis or in the veiled displacement system of Schwendener. As in other instances, however, the same effect may be produced by widely different causes, but the fact that the curves exhibited in phyllotaxis in the horizontal plan may be spirals of Archimedes leading on to helices on the cylindrical stem has been very generally accepted, and represented in diagrams in which concentric circles are taken in arithmetical progression.

So far, in fact, as such curves can be judged by the eye the approximation is very close, and not only so, but the curve drawn on a specimen (*cf.* figs. 2, 3, 4) is clearly more like such a construction than the theoretical log. spiral system previously postulated.

Further consideration, however, shows wide differences; thus it is clear to begin with, that the phyllotaxis helices observed on a shoot are not torsion spirals in any sense, but are merely the result of a uniform development in both lateral member and internode whereby a certain constant volume is reached and then further growth is checked. The helices are thus not produced by the uniform growth of all the lateral members which are initiated at different times, and would, if the rate of growth were constant in all, remain always unequal, but they are the result of a progressive *cessation of growth*,—that is to say, the helices are of secondary origin, and any spiral series of members, whatever the primary

PLATE IX.
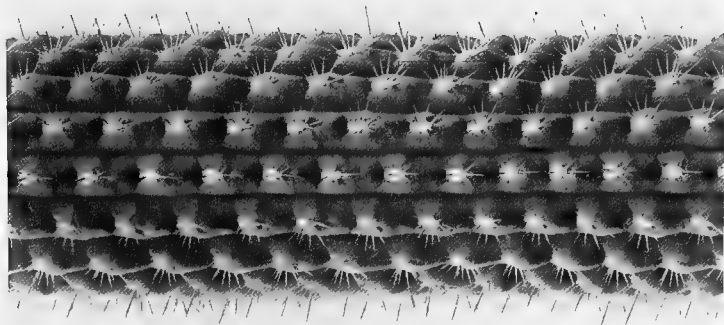
Fig. 30. — *Cereus chilensis* (7 + 9).
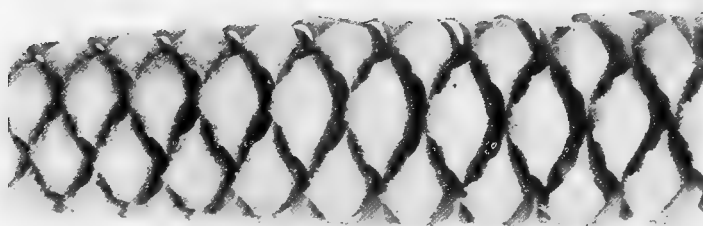
Fig. 29. *Stangeria paradoxa.* Staminate inflorescence (4 + 5).

PLATE X.

FIG. 32.—*Araucaria*, sp. $(5+8)$.
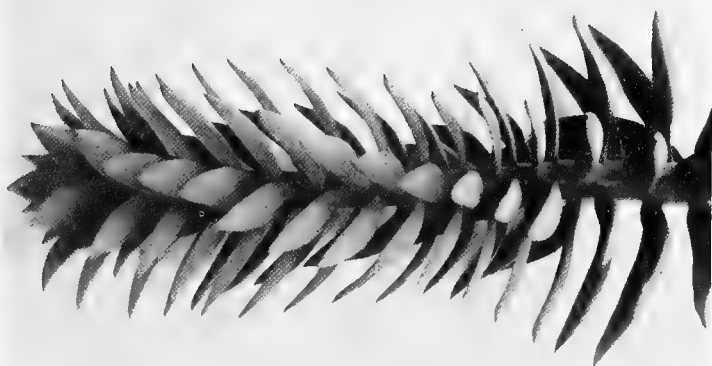
FIG. 31.—*Euphorbia biglandulosa* $(3+4)$.

spiral curve may be, must necessarily pass into a parallel screw thread type when all the members become and remain equal.

If the helices are secondary productions, it is very possible that the Archimedean spirals which would represent them on a plane system are equally secondary. The fact that a stem may go on producing leaves to infinity, without producing a terminal member, and that the leaves develop as similar primordia, is alone sufficient to suggest that the genetic spiral is a log. spiral, rather than a spiral of Archimedes which winds directly to the centre of the system and allows for no further development.

From the equation to the spiral of Archimedes ($r = a\theta$), by taking a as different values of the 2, 3, 5, 8 series, while r and θ are constant, it is easy to construct a series of spirals to correspond to these ratios (fig. 33).

In such a series the intersections of successive members of the series, drawn in the opposite direction, are seen to be, in accordance with the closeness of the ratios $3 : 5 : 8 : 13$, etc., practically identical within the limit of construction error.

A tracing from such a pair may therefore be used to map a system corresponding to the data observed in the given plant, either as a symmetrical or asymmetrical construction.*

In such a diagram it is at once observed that the intersections are not orthogonal, and therefore afford no clue to the distribution of pressures; while the rhombs are relatively much flatter at the circumference, but become very steep towards the centre : so steep do they become as all the spirals fall into the centre, that not only cannot they be adequately represented in the diagram, but it is at once obvious that it is impossible that such rhombs can in any way indicate the structure of the actual primordia arising on a growing apex, which are either isodiametric or elongated tangentially.

---

* A familiar example of the former is seen in the chasing on a watch-case, and will serve to illustrate the weak points of the system.

These curves also present a beautiful example of a subjective effect produced by an indirect method of construction.

Engraved as wavy circles which have radii differing by a constant increment, the sloping curves fall into series as spirals of Archimedes ; the number of waves being constant in each circle, the construction is symmetrical and the spirals thus appear equal in number in either direction.

For expressing the facts of actual development, Archimedean spirals are therefore absolutely useless. But while this is so, the progressive flattening of the rhombs at the periphery of the system bears a remarkable similarity to the phenomena observed in the progressive dorsiventrality of foliage leaves, and it is to this fact,
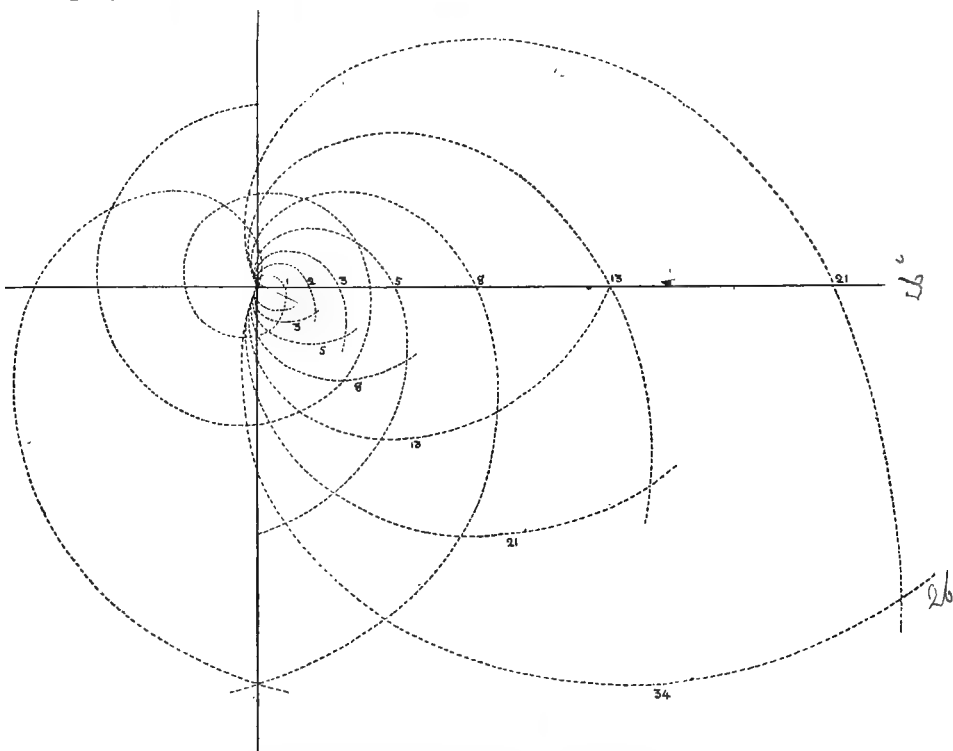
Fig. 33.—Geometrical construction for spirals of Archimedes, asymmetrical and symmetrical pairs, $a = 2$, 3, 5, 8, 13, 21, 34.

combined with the production of members which attain a fairly constant bulk, that the close approximation to an appearance of Archimedean spirals is due as the members attain their adult form.

In fact these spirals appeal to the eye, in the macroscopic appearance of such a plant as *Sempervivum*, or the cone of *Pinus*, because the members observed cover a fairly uniform area; and the parastichies approach Archimedean spirals in a transverse view

for the same reason as the curves become helices on a cylindrical stem.   As soon as the section of the actually growing primordia is observed, the resemblance to spirals of Archimedes vanishes.

Whether the log. spiral system is so far satisfactory or not, it is thus quite evident that helices and spirals of Archimedes will not satisfy the requirements of ontogenetic observation ; the ultimate approximation to such curves is a secondary phenomenon ; and with the rejection of helices and Archimedean spirals, as implying anything more than a subjective effect, *must disappear all prejudices in favour of the application of hypothetical torsion-agencies.*

V. Ideal Angles.

THE "IDEAL ANGLE."

As previously indicated, the mechanical problem set the plant in building up a system of lateral members is primarily dependent on the fact that the phylogenetic tendencies limit the apex to the construction of one member at a time; but, with this restriction, radial symmetry is required in the structure as it progresses. The corresponding metaphor would thus be the one of *building a cylindrical chimney, placing one brick at a time, and yet keeping the top always level.* To meet such a difficulty, it is clear that growth must oscillate from side to side, and that Hofmeister's law is a very good expression of the phenomena observed.

From his fractional series of divergences, $\frac{1}{2}$, $\frac{1}{3}$, etc., Schimper deduced the "ideal angle," and the brothers Bravais suggested that this angle, 137° 30′ 27″·936, an angle irrational to the circumference, might be regarded as the sole angle of normal phyllotaxis, and the same line of argument has been followed up by C. de Candolle. With the formation of other fractional series, other "ideal angles" were added, and the importance of the first one proposed became much impaired, while the possibility of there being several "ideal angles" appeared very like a contradiction in terms. All these angles followed from summation series expressing values of continued fractions of the type

$$\cfrac{1}{x + \cfrac{1}{\bar{1} + \cfrac{1}{1 + 1, \text{ etc.},}}}$$

where x might be any whole or fractional number.

It has been noticed that a remarkable interpolation of the theory

of leaf-distribution, and the tendency to a biological interpretation of phenomena, is responsible for the hypothesis that a nearer and nearer approach to the "ideal angle" of each series implied a better distribution of leaves in relation to their external environment, by preventing overlapping. The suggestion that biological aim on the part of the plant may to a great extent control the protoplasmic mechanism of phyllotaxis cannot be wholly neglected; and the formation of a "concentration-system" has already been placed in such a light, although it was not necessarily accepted as proved. But it cannot be too strongly insisted, that in any spiral, that is to say, any asymmetrical series, whatever unequal ratios the parastichies may have, every system is equally an ideal one so far as leaf-distribution is concerned, in that no two leaves are ever vertically superposed within the limit of practical observation and construction, a fact which follows from mathematical deduction and geometrical construction by log. spirals.*
Every asymmetrical system equally obeys Hofmeister's law, the logical consequence of which is, again, that no superposition ever takes place. The whole theory of an ascending series reaching to a perfect type of leaf-distribution thus falls to the ground; and not only so, but the symmetrical condition, which has been put forward as possibly the true aim of the plant, implies an actual formation of vertically superposed series of members, and therefore, according to the original hypothesis of Bonnet, an immediate departure from the maximum exposure. Nor is there any reason to doubt that biological causes may induce such a result, when the maximum exposure ceases to be the optimum; the remarkable production of a decussate phyllotaxis in the assimilating shoots alone of types which show other xerophytic adaptations being the most obvious example.†

Wiesner,‡ who approached the subject from this very standpoint of leaf-distribution, was led to very remarkable results.

He pointed out that the series in which x had a minimum value

---

* *Cf.* note on *Mathematical Orthostichies.*

† *Cf. Clematis, Labiatae, Euphorbia Lathyris, Jasminum nudiflorum, Crassula perfoliata.*

‡ *Flora,* 1875, Nos. 8 and 9.

(2) gave *the most equal distribution of leaves on an axis*, and made use of the minimum number of members. Although Wiesner's views were thus brought into line with Schimper's series, $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, etc., and pointed to the ideal angle 137° 30′ 28″, it is clear that his generalization implies much more than the simple statement that this angle is better than any of the limiting angles of other series. With a given number of leaves, this angle gives the optimum approach to a symmetrical construction; that is to say, reverting to the metaphor of building one brick at a time, this angle gives the optimum method of oscillation across the system while laying down the stated number of units, so that radial symmetry is most nearly attained. Radial symmetry is, in fact, the grand aim, and not the biological requisitions of leaf-distribution, which would be equally well served by any other series, and, when unsatisfactory, may be readily compensated by secondary zones of elongation either in the main axis or in the lateral members themselves.

To suit the theory of Schimper, Wiesner made $x = 2$; but the same results obviously follow when $x = 1$, since the ratios $\frac{1}{2}$, $\frac{2}{3}$, $\frac{3}{5}$, $\frac{5}{8}$, etc., are all complementary of those of the previous set, and the limiting angle $\left(\frac{\sqrt{5}-1}{2} \right)$ of 360° = 222° 29′ 32″ is the inverse angle of 137° 30′ 28″.*

The objection previously taken to the Schimper-Braun theory series of fractions was that they were used either to express angular measurements which could not be measured, or orthostichies which could not be proved to be vertical. It has now been seen that the so-called orthostichies are, in all cases of asymmetrical phyllotaxis, themselves log. spiral curves, and the divergence angles between them are therefore contained by curved lines. In theory, the angular measurements still hold,† but they not only become im-

---

* The curious fact that the ratio $\frac{\sqrt{5}-1}{2}$ is also that by means of which Euclid constructed the pentagon $\left(\sin 18° = \frac{\sqrt{5}-1}{4} \right)$ formed the subject of botanical speculation on the part of Kepler in 1611. Ludwig, "Weiteres über Fibonaccicurven," *Bot. Centralb.*, 68, p. 7.

† *Cf.* note on *Oscillation Angles.*

possible of observation, being contained by spiral curves, but also of representation on a diagram when the curve equations are not given. Similarly, the "orthostichies" cannot be represented on the diagram until the form of the log. spiral is known. It has further been shown that each of the determining ratios of the Schimper series comprises two log. spirals which have, as a rule, no simple relation to each other, so that neither can be drawn while each is imperfectly defined.

The system can only be accurately planned by the parastichy ratios, which, on the other hand, are much more readily observed than an ambiguous orthostichy; while, in addition, the fact that the curves used form a mutually intersecting orthogonal pair admits of a simple method of geometrical construction.

The method of presentation by means of angles of divergence and "orthostichies" must therefore be placed wholly on one side, and it is, at the same time, clear that all observations on phyllotaxis constants, in which this method has alone been used to determine them, are open to considerable error.

The parastichy ratios will therefore be alone used to define any given system, and the normal system thus becomes:—

Ps. $= (1+1), (1+2), (2+3), (3+5), (5+8), (8+13), (13+21)$, etc.

By tabulating these as simple ratios, the idea of angular divergence is eliminated and a further fact is brought into prominence:—

$$1 : 1 :: 1 : 1$$
$$1 : 2 :: 1 : 1·5$$
$$2 : 3 :: 1 : 1·666$$
$$3 : 5 :: 1 : 1·6 \; 66$$
$$5 : 8 :: 1 : 1·625$$
$$8 : 13 :: 1 : 1·615$$
$$13 : 21 :: 1 : 1·619$$

and the limiting ratio

$$2 : \sqrt{5}-1 :: 1 : 1·618$$

The simplest summation series thus implies a practical constancy of parastichy ratios in its higher terms, while the axis and the lateral primordia may be variable quantities.

Expressing this practically, in terms of the spiral-vortex

metaphor,—in any Angiosperm apex, whatever its bulk and the relative size of the primordia placed on it, the same system of curved lines of equal action is normally utilized, and the construction may thus be planned, within an extremely small range of error, with the same log. spiral curves, for all but the lowest terms of the series; further, any other parastichy ratio which approaches 1 : 1·62 may be built up with the same curve, but
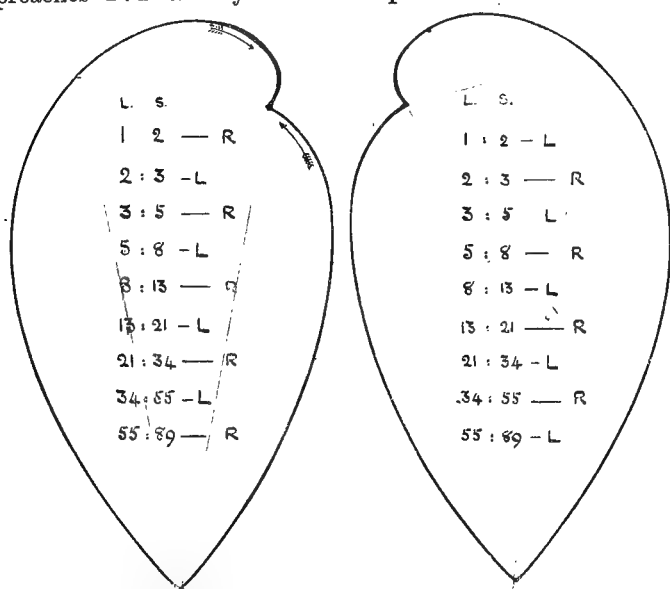
L.	S.			L.	S.		
I	2	—	R	I	2	—	L
2 :	3	—	L	2 :	3	—	R
3 :	5	—	R	3 :	5		L
5 :	8	—	L	5 :	8	—	R
8 :	13	—	R	8 :	13	—	L
13 :	21	—	L	13 :	21	—	R
21 :	34	—	R	21 :	34	—	L
34 :	55	—	L	34 :	55	—	R
55 :	89	—	R	55 :	89	—	L

Fig. 34.—Table showing direction of contact parastichies, and the genetic spiral for successive systems of the Fibonacci series.   *136*

special curves must be drawn for a closer approximation to a symmetrical pair.

The theoretical interest of the table lies in the fact, that if it is the approximation of a certain ratio which is the essential point in the scheme, the appearance of other parastichy numbers becomes conceivable so long as their ratio approximates 1 : 1·618. That such is actually the case may be checked in the case of a certain proportion of the inflorescence of *Dipsacus* and *Helianthus*. The generalization of Wiesner, therefore, when applied more legitimately to morphological relations without reference to

biological conditions, acquires a greatly enhanced value, in that the ratios naturally adopted by the plant for its parastichies are those which, being the successive terms of the simplest continuous fraction $\dfrac{1}{1 + \dfrac{1}{1 + \dfrac{1}{1}}}$, etc., give the optimum approach to symmetry in an asymmetrical system.

Just as it has been previously shown that the plant in normal asymmetrical phyllotaxis makes use of—

(1) The optimum concentration system.

(2) Those ratios of a set series which more nearly approximate the symmetrical position of equality ;
so also,

(3) It utilizes that summation series of ratios which allows the optimum approach to radially symmetrical construction.

All these three factors appear then inherent in the protoplasm, and wholly independent of extraneous forces. From the fact that all of them are illustrated in *Helianthus*, for which a normal structure was postulated, they may be regarded as constituting the fundamental principles of normal phyllotaxis; while cases in which any one of them happens to be omitted or impaired may be regarded as secondary and induced by subsequent specialization or degeneration.

OTHER SERIES.

While the series $(1:2)$, $(2:3)$, $(3:5)$, etc., thus becomes the normal system for asymmetrical phyllotaxis, the fact that other continued series have been proposed, and are generally accepted, remains to be considered. At the same time, it must be pointed out that their recognition in virtue merely of the method of "orthostichies" is wholly unreliable, and it is only in those cases in which the fractions have been determined by the method of parastichies that the ratios can be regarded as correct. Many such cases were recognised by the latter method by the brothers Bravais, though more recently the orthostichy method has been considered the most important (Schwendener, Weisse). Further, since such cases, though widely distributed, are relatively less

common, and are met with in anomalous specimens of plants other-
wise exhibiting the normal series, and especially in plants growing
under unfavourable conditions of environment, it is extremely
doubtful whether the determination of any particular set of
parastichy ratios affords any adequate reason for constructing a
series to contain it.

Such series expressed in the Schimper form are—

$a.$	$\frac{1}{3}$,	$\frac{1}{4}$,	$\frac{2}{7}$,	$\frac{3}{11}$,	$\frac{5}{18}$,	·	·	·	·	$99°\ 30'\ 6''$
$b.$	$\frac{1}{4}$,	$\frac{1}{5}$,	$\frac{2}{9}$,	$\frac{3}{14}$,	$\frac{5}{23}$,	·	·	·	·	$77°\ 57'\ 19''$
$c.$	$\frac{1}{5}$,	$\frac{1}{6}$,	$\frac{2}{11}$,	$\frac{3}{17}$,	$\frac{5}{28}$,		·	·	·	$64°\ 4'\ 43''$
$d.$	$\frac{2}{5}$,	$\frac{5}{7}$,	$\frac{7}{12}$,	$\frac{12}{19}$,	$\frac{19}{31}$,	·	·	·	·	$151°\ 8'\ 8''$

In the form of parastichy ratios—

$a.$ 1, 3, 4,   7, 11, 18, 29, 47.
$b.$ 1, 4, 5,   9, 14, 23, 37, 60.
$c.$ 1, 5, 6, 11, 17, 28, 45, 73.
$d.$ 2, 5, 7, 12, 19, 31, 50, 81.

Expressed in the former system, by turns of the genetic spiral and
indefinite orthostichies, the fact is elicited that the first three tend
to a smaller limiting angle than the normal series, while the last
(d) approaches a larger one; but when expressed as parastichies, it
becomes clear that from the standpoint of an approach to symmetry
they form very uneven systems. In the higher terms the ratios
are practically identical with those of the normal series $(1 : 1·6)$:—

(a)
$3 : 4 :: 1 : 1\dot{3}$
$4 : 7 :: 1 : 1·75$
$7 : 11 :: 1 : 1·571$
$11 : 18 :: 1 : 1·\dot{6}\dot{3}$
$18 : 29 :: 1 : 1·61$
$29 : 47 :: 1 : 1·62$

(b)
$4 : 5 :: 1 : 1·25$
$5 : 9 :: 1 : 1·8$
$9 : 14 :: 1 : 1·\dot{5}$
$14 : 23 :: 1 : 1·642$
$23 : 37 :: 1 : 1·608$

(c)
$5 : 6 :: 1 : 1·2$
$6 : 11 :: 1 : 1·8\dot{3}$
$11 : 17 :: 1 : 1·5\dot{4}$
$17 : 28 :: 1 : 1·647$
$28 : 45 :: 1 : 1·607$

(d)
$2 : 5 :: 1 : 2·5$
$5 : 7 :: 1 : 1·4$
$7 : 12 :: 1 : 1·714$
$12 : 19 :: 1 : 1·583$
$19 : 31 :: 1 : 1·632$

and this is borne out by the observation that these higher numbers are found, intermingled with the normal series, in such inflorescences as those of *Helianthus*, and especially of *Dipsacus fullonum*. Others are met with in the leafless *Cactaceae*, bractless spadices of *Aroids*, and xerophytic types, species of *Lycopodium*, *Sedum*, *Euphorbia*, etc.

Only in some of the lower terms is any marked advance toward symmetrical curve-construction exhibited; *e.g.* (3 : 4), (4 : 5), and (5 : 6). Cases in which such types occur are again no commoner than even closer approximations to equality, for which the necessity of constructing continuous fractional expressions is still less apparent. Thus :—

Parastichies	(3+4)	Ratio 1 : 1·3̇	*Echinocactus Williamsii* (with 2/3).
	(4+5)	,, 1·25	*Stangeria paradoxa*, ♂ cone ; ♀ cone also 4/5/9. *Echinocactus Williamsii.* *Pothos* spadix (Bravais).
	(5+6)	,, 1·2	*Cereus candicans.* *Echinopsis tubiflora* (varies 6/6).
	(6+7)	,, 1·16̇	*Acorus gramineus*, spadix (with 7/7). *Raphia Ruffia*, fruit scales (with 7/7). *Echinopsis multiplex* (with 6/6, 6/8, 6/9). *Echinopsis tubiflora* (with 5/7, 6/6, 6/8).
	(7+8)	,, 1·143	*Echinopsis Eyriesii* (with 7/7, 8/8, 7/6, 6/9).
	(8+9)	,, 1·125	*Richardia africana.* ♂ and ♀ on spadix.
	(9+10)	,, 1·1̇	
	(10+11)	,, 1·1	
	(11+12)	,, 1·09	*Cyathea Dregei* (1 specimen, C. de Candolle).
	(12+13)	,, 1·083	*Echinops dahuricus* (small capitulum).
	(13+14)	,, 1·079	*Echinocactus* sp. secondary effect by addition of new ridges.
	(14+15)	,, 1·071	*Acorus Calamus* (with 15/15).
	(15+16)	,, 1·06̇	

Also 13/15, 13/16, with 16/16, in *Echinops* capitula, 22/23 in ♀ flowers of a spadix of *Pothos*.

The exceptional occurrence of such parastichy ratios has the greatest interest when taken into account with the possible existence of intermediate conditions between the case of normal asymmetry and true symmetry, since the fact that such may be found might throw light on the causes which tend to induce symmetry; but, clearly, nothing is to be gained by formulating hypothetical fractional series to contain them.

Symmetrical construction is quite definite and stands by itself; the normal asymmetrical series, again, selects the optimum ratios for the construction of an asymmetrical system to the best advantage within certain restrictions: other ratios may requisition a more symmetrical set of curves, but at the expense of an inferior working angle (*cf.* fig. 63, (6+7).

Examination of the higher members of such series which necessarily approach the ratios 1 : (1·62) shows that they may be regarded as composite systems in which two or more ratios of the normal series are compounded: *e.g.*

$$29 : 47 = \left\{ \begin{array}{c} 21 \\ 8 \end{array} \right\} : \left\{ \begin{array}{c} 34 \\ 13 \end{array} \right\} \qquad 17 : 28 = \left\{ \begin{array}{c} 21 \\ -4 \end{array} \right\} : \left\{ \begin{array}{c} 34 \\ -6 \end{array} \right\}$$

$$23 : 37 = \left\{ \begin{array}{c} 21 \\ 2 \end{array} \right\} : \left\{ \begin{array}{c} 34 \\ 3 \end{array} \right\} \qquad 19 : 31 = \left\{ \begin{array}{c} 21 \\ -2 \end{array} \right\} : \left\{ \begin{array}{c} 34 \\ -3 \end{array} \right\} \text{ etc.}$$

It is true that such manipulation of ratios is open to the objection that it is "playing with figures"; but from such relations it follows that these systems might be expected to occur in plants which also exhibit bijugate constructions; and, in fact, most of them have been described in *Dipsacus*, the typical multijugate inflorescence, while they occur as exceptions in *Helianthus* (fig. 54), which again presents occasional bijugate capitula.*

The idea that there might be only one normal phyllotaxis series, from which all others were derived by slight deviations, ·occurred first to the brothers Bravais; and, when one recognises the possibility of the addition of new parastichy lines, one at a time, or the elision of one, as in the inflorescence of *Dipsacus* (figs. 38*a*, *b*), just as Cacti may add or lose ridges according to circumstances of nutrition, it is clear that many of these so-called phyllotaxis constants must be of local and secondary origin. Further discussion of such forms may be left until multijugate types have been more fully considered.

* *Cf.* Weisse, *Pringsheim's Jahrbücher*, xxx. p. 474.

VI. Asymmetry.

SYMMETRY AND ASYMMETRY.

THE whole subject of phyllotaxis is thus restricted to a question of the symmetrical or asymmetrical growth of the plant-apex during the process of originating the impulses which give rise to new centres of lateral growth.

That the framers of the original spiral theory were undoubtedly correct in demanding that symmetry is in all cases secondary, and asymmetry the primitive condition, is shown by comparative morphology; and transition, if not actually ontogenetic, is clearly so phylogenetically. All Phanerogams, Cryptogams and the bulk of the Algæ, with whorled series of lateral members, either commence with an asymmetrical condition or show traces of it in subsequent development; thus, among Angiosperms, in some types the vegetative system becomes symmetrical while the spiral condition is retained in the reproductive members (*Calycanthus*); in others the latter are wholly whorled, while the former retain the primitive asymmetrical condition (*Aquilegia*): even when both become wholly whorled, the presence of a pentamerous flower, or a type derived from such a structure (*Labiatae*), which is a form which does not mechanically pack in the sense that 2–3–4 and 6–merous types do, these being referable to rhomboidal and hexagonal systems, is sufficient evidence of a primitive quincuncial construction.

Among lower forms, the Dasycladaceae alone present types in which symmetrical construction possibly obtains from the earliest stages (*Neomeris*), and even in these the coenocytic structure is itself admittedly secondary.

Again, the impulses in the mass of growing protoplasm, constituting the first zone of growth, have no necessary connection with the presence of cell-walls or any subsidiary current-movements within the component cells of the apex, where these are present.*

Thus, in *Helianthus* or *Hippuris*, each impulse, when first observable, involves a whole group of cells; in *Equisetum* several impulses forming about one-third of a complete whorl of members can be definitely localized as belonging to the derivatives of a single segment of the initial cell; while in the coenocytic Dasycladaceae, the impulses are clearly independent of the non-existent cell walls, but the phyllotaxis is none the less perfect in its symmetrical relations, and bears comparison as a symmetrical concentrated type with members exhibiting cellular structure. Thus *Neomeris dumetosa* presents alternating whorls of thirty members, *Equisetum Telmateia* 30–40, *Hippuris* 6–12. Without insisting on any special dynamical interpretation of the complicated phenomena exhibited by such a living mass of protoplasm, it appears evident that the transverse components of the forces involved in the production of symmetrical phyllotaxis *may be expressed* by a diagram illustrating the uniform motion of a free circular vortex, the construction lines of which are

---

* Modern researches (Vöchting, Weisse, Schumann) have tended mainly to the observation of the actual facts of ontogeny, on the lines laid down by Hofmeister. But such methods have one weak point, they can only result in the statements of the facts observed without giving any reason for such phenomena. Thus in the case of the rise of a semi-fluid protoplasmic protuberance on a similar semi-fluid mass, it is clear that the causes which led to the initiation of such a formation are practically over so far as that protuberance is concerned, as soon as it becomes visible, and other forces may come into play quite different from the primary cause. Phyllotaxis is therefore concerned primarily with the forces which produce new-growth centres at or below the surface of the protoplasmic mass of the growing point, and suggestions as to their modes of operation can only be deduced from physical standpoints. The large broad apex (8–10 mm.) of a full-grown specimen of *Aspidium Filix-Mas* shows, in the early part of the year, the primordia of the leaves of the next succeeding year already commencing as slight elevations spaced out without any contact relations to one another in the spiral series (5 + 8). The protuberances are visible to the naked eye, without the section-cutting required for smaller buds, but no amount of observation of the facts of development will explain the reason why these elevations appear in their appointed places. (*Cf.* (3 + 5) system of fig. 35, Plate VIII.)

circles and radii. When asymmetrical, as in the more general theorem, the structure is illustrated by the phenomena of a spiral vortex, and all the lines of construction are orthogonally intersecting logarithmic spirals.

In all cases the symmetrical must be regarded as due to secondary specialization of the asymmetrical case, just as the circle may be regarded mathematically as a limiting case of an infinite log. spiral curve.

In both systems, "concentrated" and "non-concentrated" constructions may be possible: consideration of the schemes (B) and (D) shows immediately that all spiral types are more or less concentrated constructions, and that (A) and (C) are only the limiting cases in either direction. The same fact is illustrated by the numerical relations of the curves contained in the capitulum of *Helianthus* taken as a type (fig. 15), in which $(34+55)$ give the optimum concentration $(1+1597)$, the minimum. The optimum concentration, produced in an asymmetrical system by the approximation of the number of intersecting curves in either direction to equality, being thus a secondary effect of an approach to symmetry, actual equality gives the perfect symmetrical condition of scheme (C). The fact that this is the normal symmetrical case found in plants, while it is also regarded phylogenetically as a secondary specialization, is satisfactory evidence that the " *concentration* " *system is after all not due to any hypothetical biological demands of bud-construction, but the natural outcome of its evolution from a spiral series in which the claims of symmetry are expressed by an approach to equality in the number of parastichies as indicating orthogonal lines of equal action.*

The biological demand for a concentration construction is thus as completely eliminated from the study of phyllotaxis as Bonnet's original biological demand for equal transpiration space has already been seen to be unnecessary.

The terms " symmetrical " and " asymmetrical " are further preferable to the older corresponding terms " whorled " and " spiral," in that it will appear, as Sachs suggested, *all spiral appearances are subjective,* and not the representation of any spiral aim on the part of the plant; while the term " whorled " can only paradoxically

include the symmetrical formation of one member only at a node.

Four types may thus be distinguished—

(1) (Normal phyllotaxis) *Asymmetrical concentrated.*
(2) (Specialized phyllotaxis) *Symmetrical concentrated.*
(3) *Asymmetrical least-concentrated.*
(4) *Symmetrical non-concentrated.*

While the consideration of primary phyllotaxis will be completed by reference to

(5) *Multijugate Types.*
(6) *Anomalous Types,* including ratios other than those of the normal series.

(To be continued.)

On the Relation of Phyllotaxis to Mechanical Laws.

By

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

Lecturer in Natural Science, Jesus College, Oxford.

PART II.

ASYMMETRICAL AND SYMMETRICAL PHYLLOTAXIS.

In the previously published chapters,[*] the theory was elaborated that the arrangement of lateral members on a shoot-apex was possibly the expression of the symmetrical or asymmetrical distribution of growth-energy in the growing apex, and in a system for which uniform growth was postulated, the appearances were to be mapped in terms of the phenomena of vortex construction, and represented graphically by the same *geometrical construction* as the lines of equal pressure and flow in circular or spiral vortices respectively.[†]

That such conditions of uniform growth do not obtain to any great extent in a plant-apex is sufficiently obvious, since the apex is never absolutely plane, nor again do the curves seen in a

---

[*] *On the Relation of Phyllotaxis to Mechanical Laws.* Part I. Construction by Orthogonal Trajectories ; A. H. Church, 1901, pp. 1–78. *Cf.* Note on Phyllotaxis, *Annals of Botany,* vol. xv. p. 481, 1901.

[†] The relation of logarithmic spirals to phenomena of growth is very neatly expressed in a mathematical form, in that in two dimensions the logarithmic spiral is the only curve in which one part differs from another in size only but not in shape. This property naturally follows from the definition of an equiangular spiral, but it brings out very vividly the essential character of such a curve as a line of growth.

section cross at right angles throughout the entire area. On the other hand, the approximation to orthogonal intersection increases as the centre of the system is approached, and on every curved surface a portion may be regarded as a plane, if it be taken sufficiently small. Although the conditions of uniform growth do not obtain therefore in the whole system, it is a legitimate hypothesis that they become more and more so at the initial growth-centre, and that for practical purposes the laws of uniform growth may for the present be assumed approximately constant on the portion of the apex which is flat.

At the same time it is clear that the consideration of uniform growth must precede that of varying and diminishing rates of growth; and in the general discussion of primary phyllotaxis phenomena, uniform growth may thus be assumed to obtain at some point however small, at the apex of a plant, in the First Zone of Growth in which new growth-centres are being initiated independently of cell-structure, before the primordia they produce become visible on the surface of the protoplasmic mass.

It was further pointed out that the necessity for a new method of construction arose from the fact that, granted that such lateral members as the leaves on a shoot arose as *similar protuberances*, and under conditions of uniform growth would always remain so, it was not mathematically possible to place a spiral series of such bodies in contact on a plane surface in strict terms of the divergence formulæ of Schimper and Braun, which were again originally postulated for cylindrical systems.

Very close approximations to the true curve may be found in shoots which show little longitudinal extension, and may be plotted from sections of the plant in the rosette condition. For example, in a section of the broad apex of a perennating rosette of *Verbascum Thapsus* (fig. 36), the curve drawn empirically through the centres of the leaf-members is very similar to the true curve, differing only in the fact that it is a little shorter radially.*

* In making such preparations a general method has been adopted which appears to give sufficiently satisfactory results. Hand-cut sections of spirit-material are cleared in potash and Eau de Javelle, and thus restored very
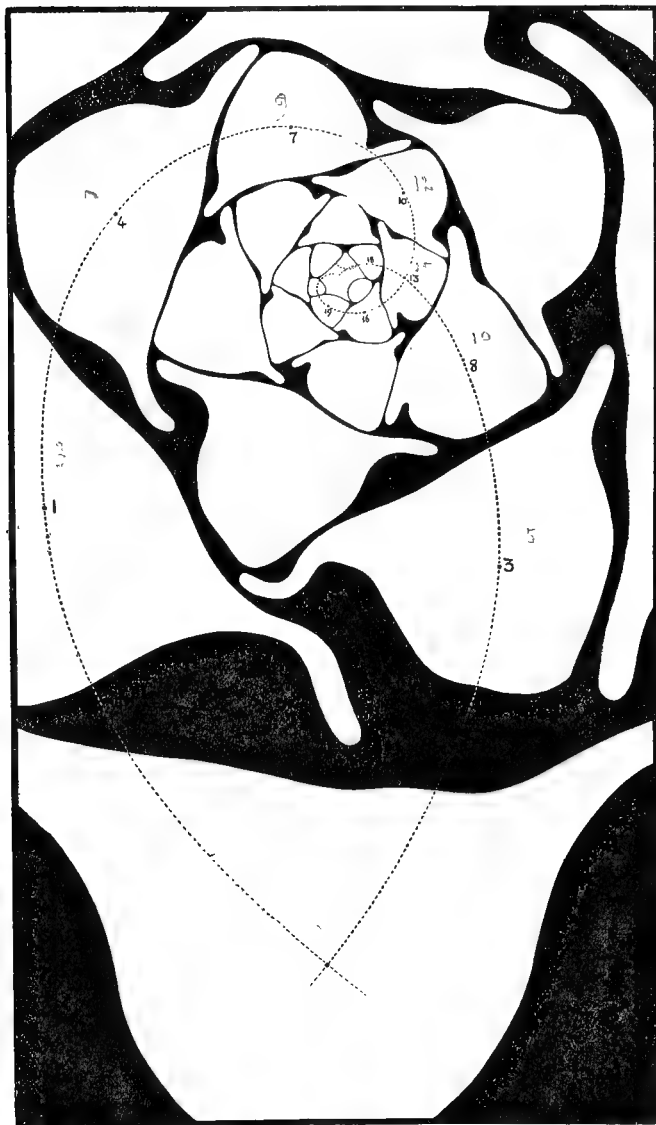
Fig. 36.—*Verbascum Thapsus*, L.   Transverse section of the apex of a perennating shoot: system (3 + 5).   The curve drawn through empirical central points of the leaf sections approximates the true curve of uniform growth very closely (cam. lucid.

The special cases of phyllotaxis may now be considered under the headings :—

(1) Asymmetry of the normal Fibonacci series.

(2) Symmetrical construction, in which the Fibonacci ratios are lost.

(3) The special case of "Least concentrated" asymmetry.

(4) Non-concentrated symmetry.

While separate sections will be devoted to—

(5) Multijugate systems.

(6) Anomalous systems.

Subsequent sections will include the consideration of secondary disturbances in the primary system, the relations of dorsiventral primordia, deductions from the mathematical investigation of the log. spiral systems, and the relation of all these factors to the interpretation of floral structures in the form of floral diagrams.

nearly to the volume occupied when fresh.   By making a careful camera lucida drawing on a large scale, about 12 ins. by 8, the construction lines can be followed with a considerable amount of accuracy.   The diagrams are subsequently blocked in with a brush, as the contour is thus more accurately kept than by a pen.   The errors of the diagrams are due to—(1) contraction of the spirit-material ; (2) error of the lens and camera lucida ; (3) error of cutting the section strictly transverse.   The last mentioned, being judged only by eye and hand, is clearly the greatest source of error, and can only be eliminated by comparison of several sections.   On such figures, distances can be measured in millimetres, and angles to half a degree, with a reasonable amount of accuracy.   All the figures used as illustrations are much reduced in reproduction.

I. Normal Fibonacci Phyllotaxis.

THE type corresponds to the case of cycles in spiral series derived by Schimper and Braun from the fractional series of divergences by the assumption of slight hypothetical "Prosenthesis," and by Schwendener from the same fractional series by equally hypothetical "contact-pressures."

It can only be strictly defined by the number of intersecting parastichies, the ratios of which mark successive values of the stages of the continuous fraction $\dfrac{1}{1 + \dfrac{1}{1 + \dfrac{1}{1}}}$, etc., and is figured diagrammatically by the corresponding number of log. spirals drawn with the appropriate curve tracing of the series 1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, etc.

From the fact that this is the system found in the Sunflower, which was regarded as *par excellence* a normal plant, it may be regarded as the normal type for all Phanerogams, without necessarily implying that it is also the phylogenetically primitive one.

Since the construction diagrams are correct well within the error of drawing, and far within that of any actual observation on the plant, geometrical plans may be utilised for the further investigation of the properties of such a system.

Since also the spiral construction (Scheme D*) was derived geometrically from the symmetrical case (Scheme C), and that for all mathematical deductions from the latter case, homologous pro-

* Part I., figs. 22, 23, p. 51.

positions will hold for the asymmetrical condition, and since, again, uniform growth in a plane circular system may be indicated by a series of "circles" enclosed in a "square" meshwork, in which successive "squares" and "circles" are in geometrical progression, it follows that growth is equally uniform throughout the spiral system, and successive members along any spiral path are also in geometrical progression.   These relations, following from the system of construction, are indicated for a $(3+5)$ system in fig. 28.

Although circles have been inscribed in the orthogonal areas, it is clear that the proper figure which only becomes a circle as the orthogonal area becomes a square, is of an "ovoid" form,* while a point which may be found for each area by drawing twice the number of curves in either direction, and therefore represents the intersection of the intermediate spirals, will at the same limit become the centre of the circle.   It may be now termed the "*Centre of Construction*" of the ovoid.   These centres of construction fall on circles the radii of which are again in geometrical progression, and growth in each lateral member is uniform with that of the circle which represents the main axis; and in such an expanding system, circles drawn through the centres of construction of the lateral members will indicate the relative size of the axis when the member was laid down.   Since growth is uniform throughout the system, this ratio is a constant and may be used to define the system; and for the same reason, the same diagram which expresses the relative size of the developing primordia will also represent the relative position of the areas in which the first impulses originated as possibly mathematical points corresponding to the centres of construction.   The ovoid figures approach circles so closely when the angle they subtend is small, that the error is almost beyond the error of drawing; below 60° it is practically unnoticeable, and the inscribed curves may be thus represented by actual circles.   At the same time it must be remembered that, though these figures are in a spiral system ovoid curves in their relation to the parent axis, they represent growth-centres with a partially individualised activity, and may therefore by their own

---

* *Cf. Mathematical Notes*, for the equation and construction of the true curve.

inherent growth movements tend to become circular in section, as for example they would if they were merely semi-fluid masses contained in a uniformly elastic membrane.

A circle inscribed within the orthogonal area with a definite centre of its own, which is not the true centre of construction, may be thus
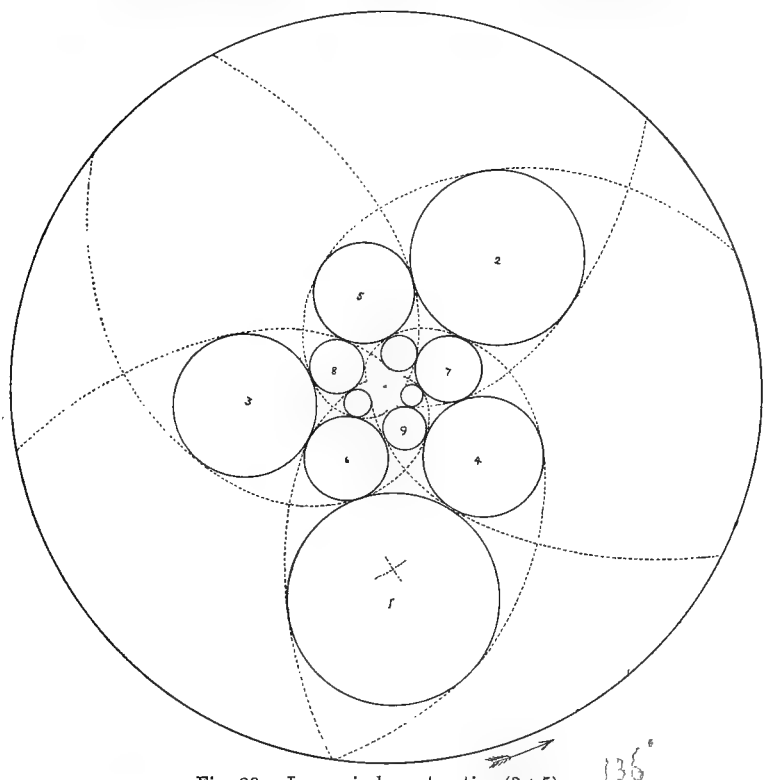
Fig. 28.—Log. spiral construction (3+5).

taken as representing the actual primordium within the error of drawing or observation.

Since also the true curve is an ovoid, and the ratio of distances between the new growth centres must be measured along the

* That is to say, since comparison can only be made between similar figures. *Cf. Mathematical Notes.*

spiral paths which pass to infinity, a method may be adopted which gives a mean ratio with approximate accuracy, dependent on the initial error of drawing the curve-systems; and although destitute of any strict mathematical value, a simple method of comparing the ratios of the lateral members to their parent axis is obtained, if this secondary circle and growth-centre be regarded as representing the lateral member, and affording a mean value of distances which in the limit approach equality. Thus in the $(3+5)$ system (fig. 28), measurements may be taken in millimetres from a carefully constructed figure within the error of drawing the true log. spiral. In the case figured, the radius of the circle representing member 1 was 22·5 mm., while the distance between the centre of this circle and the centre of the whole system was exactly 45 mm., and since all the orthogonal areas are similar, the ratio is a constant for every member and equals 1 : 2.*

Taking this ratio as a sufficiently correct approximation, *a (3+5) system is thus the natural consequence of a spiral-vortex construction when the diameter of the primordium of the lateral member is one-half that of the axis at the point on which it is apparently inserted.*

Again, by using the *metaphor* of an actual spiral-vortex movement, it is clear that the impulses which originated in the fluid mass of protoplasm may be regarded as at first of the nature of mathematical points from each of which a new vortex motion was initiated, expanding in all directions until it came into contact with adjacent vortices; further expansion in each would then result in the heaping up of a mass of protoplasm which becomes the obvious external sign of the origin of a new member.†

The diameter of the primordium is thus only the expression of *the distance between the new impulses,* and it is the ratio of such distances to the diameter of the main axis which is the fundamental constant which determines subsequent phyllotaxis phenomena. As

---

* *Cf. Mathematical Notes.* More accurately the ratio may be taken as 1 : 1·95, the amount of error in the geometrical construction being $\frac{1}{39}$th.

† Hofmeister pointed out that the position of new members might be indicated by changes in the tensions of the superficial cells before any elevation of a primordium was observable.

there is no evidence that there is any real vortex *movement* in the protoplasm, the hypothesis that the lateral primordia must be necessarily produced in close lateral contact cannot be maintained on these grounds, and it does not follow that the ratio of the diameters of axis and primordium will adequately represent the distance-ratio of the new impulses.* Thus in the broad flat apex of *Aspidium Filix-Mas*, the new primordia arise obviously at points spaced at a considerable distance from each other, and yet fall along the well-defined paths of a $(5+8)$ curve system. $(3+5)$, fig. 35†; *cf.* also *Sempervivum*, fig. 82; *Nymphaea*, fig. 94.)

Although in such cases the elevation of the protuberances may be imperceptible at their periphery, it is probable that each primordium is strictly localized from the first at or below the surface, even if this is not obvious to the eye, and in the great majority of cases the actual close lateral contact of the primordia is undoubted. The ratio of the diameter of the axis to that of the primordium arising on it may therefore be conventionally used as a constant and may be termed the *Bulk-ratio*.

---

* It will be noticed that this view of *bulk-ratio* is an entirely artificial one, and can only be useful so far as it is regarded as a convention which may make discussion easier. Widely differing results are given when comparison is made between the area of the true ovoid curve and that of the circle drawn through the *centre of construction*, which is the true centre of insertion. Two standpoints are involved : one, that of the completed system in which the bulk reached by the lateral members may acquire some relation to that of the axis on which they are inserted ; the other, that of the similarity of growth-extension from all growth-centres. In the former case, each lateral member would be regarded as possessed of a certain relative size to begin with, and the same view would be adopted so long as the growth may be considered uniform, since one part cannot grow faster than another. In the latter, granted an increased rate in the lateral members, each lateral growth-centre would continue to expand uniformly until contact was made with adjacent members ; ultimate extension would thus be only limited by the distance between adjacent impulses ; and this for a $(1+1)$ system, for example, is relatively enormous.

The importance of such lateral contact has been emphasised by Schwendener, and it obtains in the vast majority of constructions ; but it is also clear that in a system for which the rate of growth is not uniform, the growth of a lateral primordium might be so affected that contact may either never be established or only be attained at a subsequent stage. (*Aspidium.*)

† Part I. Plate VIII.

Examination of similar diagrams, constructed with the same approximately correct curve, shows that these ratios follow the same ascending series.

Thus actual measurements gave:—

		mm. mm.	
$(3+ 5)$	.	$22\cdot5 : 45$ or very approximately $1 : 2$
$(5+ 8)$	. .	$18\quad : 54\cdot5$ . . .	$1 : 3$
$(8+13)$	. .	$12\cdot5 : 62\cdot5$ . . .	$1 : 5$
$(13+21)$	. .	$8\cdot5 : 68\cdot5$ . . .	$1 : 8$
$(21+34)$	. .	$5\cdot5 : 72\cdot5$ . . .	$1 : 13$
$(34+55)$	. .	$3\cdot8 : 75\cdot5$ . .	$1 : 21$

As the error of measurement increases with the rise of the series, it may be assumed that $(55+ 89)$ corresponds to $1 : 34$

$$(89+144) \qquad ,, \qquad 1 : 55$$
$$(144+233) \qquad ,, \qquad 1 : 89$$

With the lower ratios $(2 + 3)$, $(1 + 2)$, $(1 + 1)$, the error of construction becomes obvious, since circles cannot be inscribed in the "squares" to represent the ovoid curves with sufficient accuracy.*

, Lateral primordia are thus to be regarded as bodies presenting a definite bulk; and since the last given ratios are the highest known in the plant, it follows that, in dealing with bulky primordia, in contradistinction to the mathematical points and series tending to approach an "ideal angle" of the Schimper-Braun theory, such a limitation of the series while the bulk of the lateral member is still relatively considerable, must admit of the possibility of a certain degree of structural error in the systems. This becomes more obvious when the bulk-ratio is expressed in terms of the angle subtended by a primordium.

Since the ratio of the radii of the primordium and parent axis is

---

* A comparison of these values on a carefully constructed diagram three feet in diameter, in which the error of drawing became apparent, showed that these general results hold within a very trifling error; and that this error is not much more than the difference between these results and calculated mathematical ratios. (*Cf.* Note IV.)

the sine of half the angle subtended, the previous series be-
comes :—

System.*	Bulk-ratio.	Angle-subtended.	
(3+5)	1 : 2	60°	or roughly 60°
(5+8)	1 : 3	38° 57′	39°
(8+13)	1 : 5	23° 5′	23°
(13+21)	1 : 8	14° 20′	
(21+34)	1 : 13	8° 48′	
(34+55)	1 : 21	5° 26′	
(55+89)	1 : 34	3° 24′	
(89+144)	1 : 55	2° 5′	

There is reason to believe, however, that these highest systems
are never formed directly at the apex of a young axis, but are
gradually built up along similar curve systems; and the occurrence
of such a system as (8+13) as a direct formation is the limit of
the capacity of the plant. When such a system is regarded as
composed of primordia each subtending an arc of 23°, the possi-
bility of a range of error amounting to even more than one degree
is at once apparent. It will not be necessary so far to regard the
plant as working to any divergence angle of very exact degree,
and the approximation in building the system to such an angle as
137°·5 may be very rough. This becomes still more obvious when
the ease with which the primordia make very considerable adjust-
ments is taken into consideration.

Cf. Mathematical Notes, IV.

II. Constant Phyllotaxis.

WITH such an assumption that growth is more or less uniform so long as the apex remains in the condition of Zone I., and absolutely so at some central point at which the new impulses are originated, it is possible to build up any system of phyllotaxis, the results of uniform growth being expressed by taking circles whose radii are in the requisite geometrical progression.   For example :—Taking a case in which the lateral members are assumed to have a bulk-ratio with the main axis of 1 : 2, a (3+5) system may be produced by adding one new member at a time, and allowing each to grow along the same series of circles in geometrical progression.

Fig. 37, 1, shows the insertion of one such primordium.   Now, if the second member be laid down on the side exactly opposite the first, the system assumes at once a *symmetrical* condition, and the symmetrical construction of one member at a node thus induced, giving rise to the phenomenon of exactly alternating leaves in two rows, is general among Monocotyledonous types (*Iris*, *Canna*, Gramineae.) If the axis is growing asymmetrically, however, the primordium is formed at an approximate angle of 137° on a log. spiral system, the ratio of the curves of which approaches 1 : 1·62 ; since this angle and ratio gives, as concluded from Wiesner's observations, the optimum oscillation effect in constructing the nearest approach to a radial system, one member at a time.   The second member thus falls (fig. 37, 2) on one side of the diameter passing through the first one.

As it must fall either right or left of this line, it would appear probable that the chances are equal in either case, and that in

accordance with the laws of chance, the side on which it falls, which
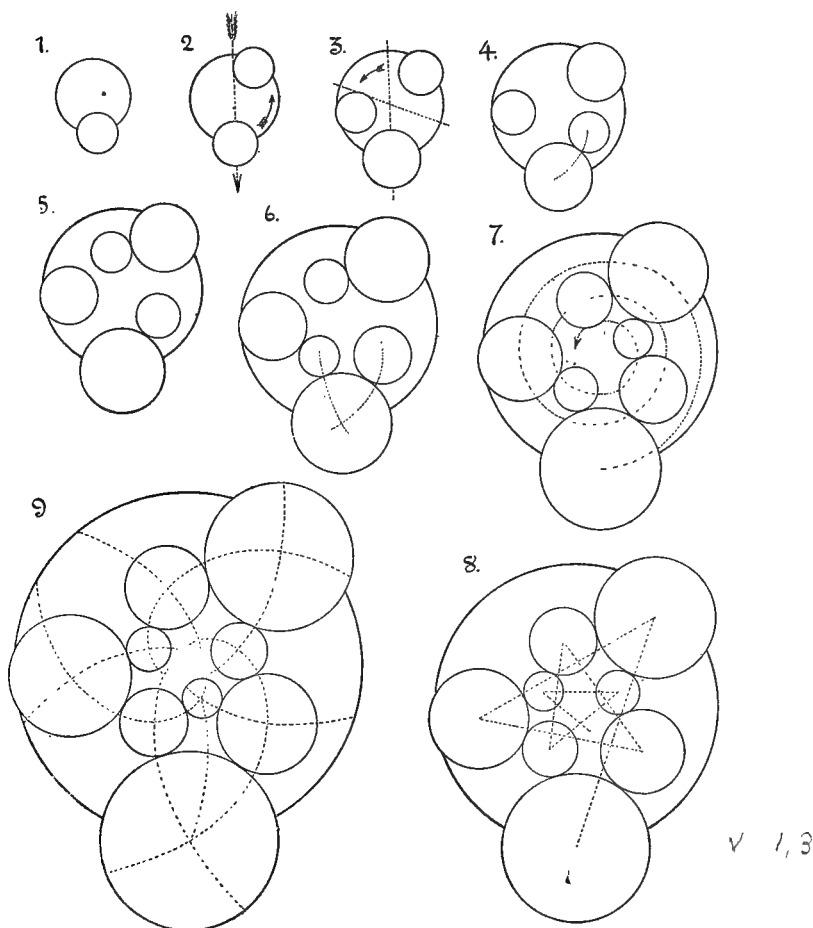
Fig. 37.—Scheme for constructing a (3+5) system by uniform rate of expansion in axis and primordia : the asymmetrical addition of one new member at a time produces a subjective appearance of spirals, or may be regarded as the result of a growth oscillation across the apex.

clearly indicates the course of the ontogenetic spiral, Right or Left, should result in the fact that, given a large number of specimens,

right- and left-hand spirals should be approximately equally dis-
tributed among them.*

* Bonnet (*loc. cit.*, p. 179) gives 43 Right and 30 Left as the result of the
examination of 73 Chicory plants, or 59 : 41 per cent.

Observations on Pine cones do not yield very conclusive results, thus :—

I. 100 cones from one tree of *Pinus austriaca* (B.G.O. 1900) were counted ;
the curves on the base of the dry expanded cone are $(8+13)$, the
direction of one of the shorter (13) curves is readily checked :
comparison of the table (fig. 34) shows that in such a system the
genetic-spiral winds in the same direction as the long curves. As the
cone is viewed from below, the spiral of the diagram will be the reverse,
or the same as that of the short curves observed. Such a set of cones
gave 59 Right and 41 Left.

II. 100 cones from one tree of *Pinus pumilio* (B.G.O. 1900) showing similar
construction gave 53 Right and 47 Left.

III. 100 cones from one tree of *Pinus laricio* (E. G. Broome, 1900), the "8"
curves being marked gave 68 Left and 32 Right.

The inequality of these numbers may therefore be the expression of the fact
that homodromy is more usual than heterodromy, and further observations are
needed.

These have been made for the same trees by Mr E. G. Broome for 1901 with
closely similar results :—1000 cones from the same tree of *P. austriaca* gave in
batches of 100 each—

R.	L.						R.	L.
54	: 46	.		.	.	(1)		
56	: 44			.	.	(2)		
51	: 49				.	(3)		
49	: 51				.	(4)	R.	L.
54	: 46	.			.	(5)	Average 53·6 : 46·4	
57	: 43	.				(6)		
54	: 46					(7)		
56	: 44	.		.		(8)		
51	: 49	.	.			(9)		
54	: 46	.			.	(10)		

Although very nearly equal, there was thus a distinct tendency in this tree
to form a right-hand spiral.

The case of the specimen of *P. laricio* was even more remarkable.

Four hundred cones were counted ; the first hundred gave a result identical
with that of the previous year, . 68 : 32

Successive batches of 100 each, . $\left\{\begin{array}{l} 75 : 25 \\ 79 : 21 \\ 63 : 37 \end{array}\right.$

Or an average of 71 Left : 39 Right, a result in which the element of chance
appears quite out of the question, so far as the members of one tree are concerned.

In the same way, the third member falls into the largest gap between members 1 and 2, but asymmetrically, being on the side of the gap farthest from the last formed member. Hofmeister's law, which is clearly a simple way of expressing what is observed in such a series of diagrams, may be thus enlarged by adding the point that *the new member falls asymmetrically* into the next largest gap.

The fourth member establishes lateral contact with No. 1, and thus initiates the first contact-parastichy—the long curve of the system, while the sixth member similarly commences the first short curve parastichy, the system being $(3+5)$; the parastichies thus appear as subjective spirals joining the centres of members in orthogonal contact (fig. 37, 9).

The subjective spiral joining the centre of successive members becomes the ontogenetic spiral (fig. 37, 7); but the growth movement is equally clearly defined as an oscillation across the apex of the stem at an approximately constant angle (fig. 37, 8).

The ninth member falling on a new log. spiral line passing through No. 1, gives the so-called " orthostichy " line of Schimper.

Of these spirals, then, the genetic spiral is of interest solely that it marks the ontogenetic path of construction; the contact-parastichy spirals are, however, structural and map out the system, in that they may be regarded as representing lines of equal and asymmetric distribution of growth-energy in the protoplasm of the apex. *These are not necessarily the cause of the appearances, but rather both phenomena are equally expressions of the fact that growth is asymmetrical, and therefore represented by the geometrical construction of a spiral-vortex.*

Uniform and Varying-growth Phenomena.

It would so far appear that the inherent property of protoplasm, which determines the phyllotaxis of lateral members, thus reduces to the fact that in every shoot the bulk-ratio of the lateral primordia, or rather the ratio of the distance between two initial points to the diameter of the axis, may be a constant, and definite for each shoot, though less definite as a specific constant. Of such

a fact the secondary parastichy curves are a necessary consequence; and the ratios that these exhibit present a remarkable analogy to the well-known phenomena observed in root-apices, in which the number of the protoxylem points which here subsequently determine the arrangement of the lateral members is also an inherent property of the protoplasm, determined for each root-apex, constant within a certain range for the species, but varying in actual branches with the amount of nutrition : for example, the constant for the typically tetrarch root of *Ranunculus repens* sinks to 3 and 2 in a weak lateral root, or rises to 5 or 6 in a strong one.   In the same manner, the foliage leaves of a shoot of a given plant may be laid down with a low number of curves, *e.g.* $(2+3)$, but in strong axes the ratio may rise to $(3+5)$, and in reduced axes may fall to $(1+2)$.   The commonly observed fact that the main axes of many plants present a "$\frac{2}{3}$" phyllotaxis, while secondary lateral ones reduce to "$\frac{2}{5}$," as first noticed by Bonnet, is thus explained by the assumption that the protoplasm of any asymmetrically growing shoot possesses a definite curve-system, usually of a low ratio, and ranging for the great majority of plants between $(2+3)$ and $(8+13)$.

In certain cases, however, as in the capitula of *Helianthus* and other Composites, the phyllotaxis ratios reach very high numbers, and these exhibit the same phenomena in correlation with the nutrition of the axis in which they obtain.   Thus, the medium capitulum of *Helianthus* taken as a type, presents $(34+55)$ parastichy curves, but in weaker plants these reduce to $(21+34)$ and $(13+21)$, while in exceptionally well-nourished plants the construction curves are $(55+89)$ and $(89+144)$.   The same progressive reduction in the curve system is also noticed in the capitula terminating lateral branches of the first and second degree.

Either, therefore, these high ratios are determined by the apex at its first formation, or a transition must take place from one series to another; the former alternative might be homologised with the production of a polyarch root in many plants, and from this point of view, the shoot of *Helianthus* might be regarded as containing a large number of potential curves, of which, if conditions were unfavourable, only a few would be utilised; and,

PLATE XI.

FIG. 38a.—*Dipsacus fullonum*, L. Distortion of parastichies consequent on adding a new curve.

FIG. 38b.—*Dipsacus fullonum*. Similar distortion effects produced by loss of curves.

PLATE XII.
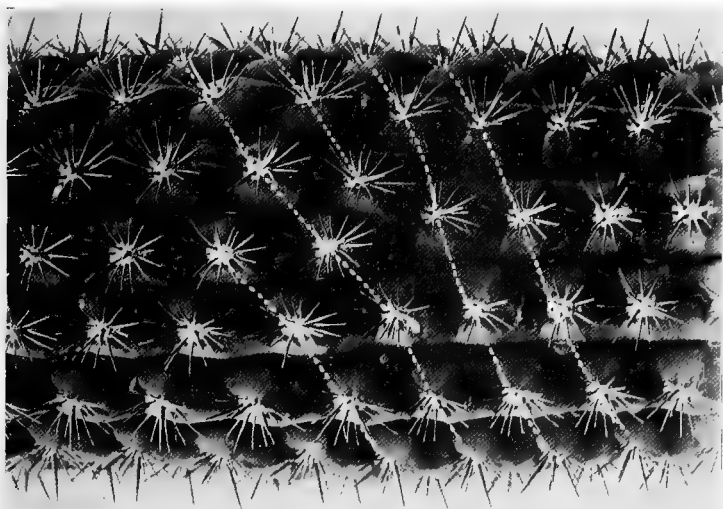
FIG. 39b.—*Cereus chilensis*, Colla. Distortion of ridges by adding a new short curve. The system thus rises from $(7+8) = 15$ ridges to $(7+9) = 16$ ridges.

FIG. 39a.—*Cereus Jamacaru*, P.DC. Reduction of ridges, $5 = (2+3)$ to $4 = (2+2)$ by loss of a curve.

when mature plants are alone considered, the fact that the total number of foliage leaves and sterile involucral scales borne on a stem is with few exceptions less than one complete cycle of floral members,* as indicated by the parastichies of the disk, shows how difficult such an idealistic conception may be to disprove.

On the other hand, seedlings of Helianthus,† well supplied with reserve food materials, evidently lay down their primary curve system under very similar conditions, and a section of the terminal bud of a young plant shows a low ratio of parastichy contact-curves, while definite contact curves of higher ratios, but yet lower than those of the disk, are seen on cutting across the involucral scales of the capitulum.

It remains, therefore, to consider the preceding curve-systems from the standpoint of—

(1) Transition from one series to another.

(2) The phenomenon already indicated as possibly representing a "rising phyllotaxis" characteristic of the involucre of Composites (*Helianthus*, fig. 14; *Cynara*, fig. 9).

To take an example of the former, the difference between a $(34+55)$ construction and that of a $(21+34)$ might be expressed by retaining the 34 long curves and reducing the short curves to 21—that is, by dropping out 34 of the latter parastichy lines of equal growth. If this be attempted on a diagram, the parastichy curves and the ontogenetic spiral still follow the same direction, but the orthogonal areas are obviously no longer "squares," and would not therefore contain the homologues of circles—that is to say, in the plant the circular primordia would be distorted to broad ellipses. The $(21+34)$ system can thus only be represented by 21 long curves and 34 short. By dropping out 11 long and 21 short from the

---

* *Cf.* Weisse, Tables of *Helianthus*, *Prings. Jahrb.*, xxx. p. 474.

† Seedlings of *Helianthus annuus* produce, beyond the cotyledons, usually 3–4 pairs of decussating foliage leaves. It is not clear why such a symmetrical construction should be found in the Sunflower and subsequently converted into a spiral system ; in allied species, however, the decussate system is continued throughout the whole of the assimilating region, but ceases at the branching of the inflorescence region (*cf. H. strumosus* and *H. rigidus*, garden varieties). When the secondary change takes place the curves $(2+2)$ become typically $(2+3)$ or $(3+5)$, rarely $(3+4)$ or $(2+4)$.

$(34+55)$ system, uneven orthogonal figures will, it is true, be produced, and it might be conceivable that the plant could adjust these to circular primordia as growth proceeded, so long as the direction of the curves remains the same, but it will be found that the genetic spiral is reversed.*
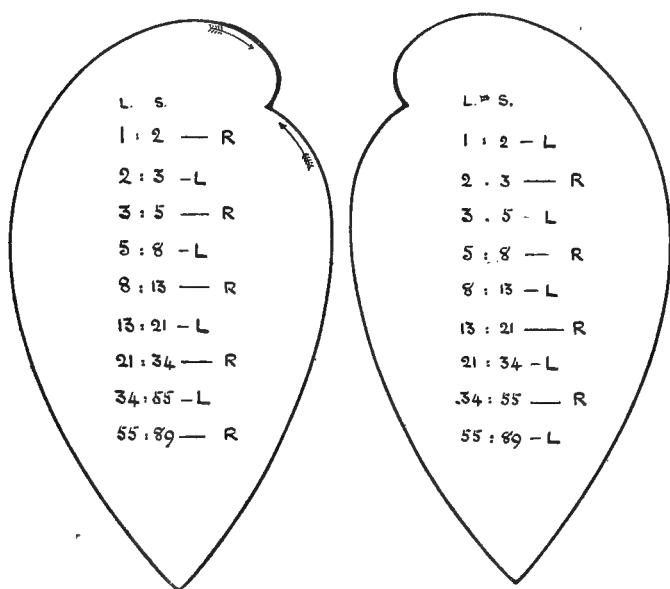
L. S.		L. S.	
1 : 2 — R		1 : 2 – L	
2 : 3 – L		2 . 3 — R	
3 : 5 — R		3 . 5 - L	
5 : 8 – L		5 : 8 — R	
8 : 13 — R		8 : 13 – L	
13 : 21 – L		13 : 21 — R	
21 : 34 — R		21 : 34 – L	
34 : 55 – L		34 : 55 — R	
55 : 89 — R		55 : 89 – L	

Fig. 34.—Table showing direction of contact parastichies, and the genetic spiral for successive systems of the Fibonacci series.

There is clearly no evidence whatever that such reversal occurs in normal growth, since the genetic spiral (*Cynara*) may be checked

* This remarkable property of the curved systems, by which the spiral selected as the ontogenetic spiral is reversed in successive ratio-systems, is tabulated in fig. 34 (Part I. p. 70). Comparison of the structural diagrams for $(5+8)$ and $(8+13)$, for example, with the same direction of parastichy curves, shows that the displacement of the first member of successive cycles in the latter case follows the direction of the genetic spiral, but in the former is in the reverse direction. These appearances may be readily checked on the dry cones of *Pinus austriaca* $(8+13)$ and *Pinus laricio* $(5+8)$.

Such reversal will again lend additional complexity to phenomena of homodromy and heterodromy in lateral shoots.

leaf by leaf.* If then in the same construction the genetic spiral remains constant, the direction of the parastichy curves must be reversed; although it is possible that the plant-apex might stop and reverse to complementary lines of equal distribution, such an arrangement would undoubtedly appear in the form of a sharp line of demarcation between the cycles, and would be recognised, if the system were continued to any distance, as a reversal of parastichies.†

There does not appear to be, then, any practicable method of passing from one cycle to the next without distortion being apparent. Thus, in the inflorescence of *Dipsacus fullonum*, a new parastichy curve may be initiated in the middle of the capitulum (fig. 38*a*), or curves may be dropped out one at a time (fig. 38*b*).

The distortion is very obvious, and appears, in the former case, to be initiated by the development of two primordia in the place of one when the error of construction, due to the greater increase of the axis bearing a constant lateral member, becomes sufficiently large. An identical phenomenon, in which a new ridge is added, or dropped out, probably in correlation with conditions of nutrition, is afforded by the stems of Cacti, the distortion produced being again considerable ‡ (fig. 39*a*, *b*).

From the standpoint of uniform growth, no transition from one phyllotaxis series to another is possible without distortion. Any such changes, therefore, when they occur, must be secondary, and the compensatory allowances must render the distortion more or less obvious.

Thus, given a certain ratio between the diameter of the primordium and that of the axis producing it, the growing apex works out the system, until, by constant repetition, certain members fall into series which give the subjective appearance of log. spiral parastichies.

Any secondary change in the system must result in the disturbance of these parastichy curves, and either appear as a " distortion " of the series, or completely break up the system.

In other words, so long, and so long only, as the ratio between axis and lateral primordium remains constant, and a given axis

---

* *Cf. Bellis* (fig. 47).

† *Cf. Saxifraga umbrosa* (fig. 52).

‡ *Cf.* Vöchting, *Prings. Jahrb.*, xxvi. 438.

produces a uniform system of members, it becomes possible to give a mathematically accurate account of the more immediate causes of the phenomena observed, in that the members, as they are formed, fall into a definite spiral system, which by constant repetition produces the subjective effect of "genetic-spiral," "parastichy" spirals, and so-called "orthostichy" spirals.

The *formal description* of phyllotaxis thus becomes restricted within very narrow limitations. As soon as the relative bulk of axis and primordium varies to any considerable extent, changes must ensue in the system, and the phyllotaxis formula becomes altered, and is only again capable of mathematical expression when the ratio once more attains constancy. At the same time it is possible to deduce from these relations the fact that the change, when it does occur in such a mechanically produced system, must normally be a gradual one, while any abrupt transition from one system to another, involving a very considerable alteration in the bulk-ratio, is undoubtedly to be regarded as the expression of an active interference in the working mechanism by the inherent form-determining properties of the protoplasm of the organism. And not only so, but such a violent disturbance of the system must be regarded as the expression of a break in the ontogenetic recapitulation of a phylogenetic change which was originally a gradual progression. Abrupt disturbances in the bulk-ratio, at any given point on a plant axis, thus imply a break in the continuity of a mechanical system of member production, which may be taken as the sign of extreme biological specialisation; and thus the production of an Aroid spadix (*Acorus, Richardia*), or the arrangement of the essential organs in certain flowers (*Clematis, Papaver, Paeonia, Cereus*), in which the relative volume of the lateral member with regard to that of the axis is abruptly lowered to a very considerable degree, indicates a highly specialised line of descent; and such rapid transition-phases of phyllotaxis cannot be accepted as expressions of the mechanical laws controlling normal phyllotaxis change, but must be considered later, when the rules governing the changes in simpler cases are understood.

PHYLLOTAXIS OF ARAUCARIA EXCELSA.

Araucaria excelsa, R. Br.—A good example of this relation of the " bulk-ratio " to phyllotaxis phenomena is afforded by such a plant-form as *Araucaria excelsa*, in which, owing to the remarkably small development of the foliage-leaves, and the absence of special growth-modifications in them, the symmetrical development of the plant is allowed free scope.

The main axis of a young plant grows erect and produces leaf-members in well-defined $(8+13)$ system, the primordia being pressed into uniform rhomboidal areas, and the transverse section shows a very close approximation to the theoretical vortex-construction.

The secondary axes are spaced symmetrically round the main stem and hence follow the Fibonacci series, 5 or 8 being the most usual. When growth is vigorous these axes similarly present the $(8+13)$ system but develop horizontally (figs. 40, 41).

Tertiary axes are produced in two rows only, along the flanks of the secondary axes, which may be so far regarded as presenting a certain dorsiventrality in the space-form of the branches. Section of the apex shows that the spiral construction is utilised and not disturbed, the lateral branches of this order being arranged along two lateral " orthostichy " lines (Phyllody spirals) towards the upper surface, the spiral character of which may be observed on the plant. It will be observed that these lateral shoots arise in the axils of two successive members of each full cycle (*e.g.*, 12, 13, and 33, 34, in fig. 40).

These tertiary axes produce leaves in the system $(5+8)$ (fig. 41), and as a general rule develop no further. But when a leading bud of a secondary axis is damaged, the end branch may assume its place and similarly produce lateral shoots in two rows. An example of such a bud whose construction showed the $(5+8)$ system gave rise to a large number of laterals, all of which were constant and homodromous at $(3+5)$ (fig. 41).

Apices of lateral branches of the first degree may also be found on the same plant exhibiting the anomalous ratio $(7+11)$ (fig. 41).
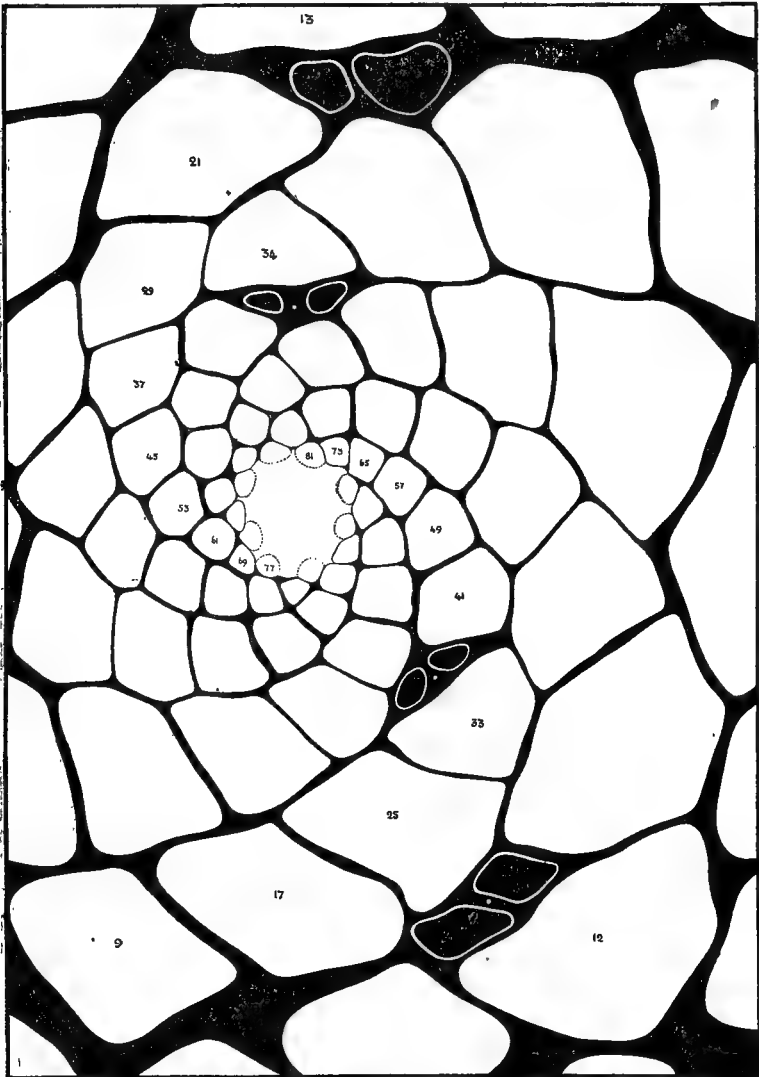
Fig. 40.—*Araucaria excelsa*, R. Br. Transverse section of the growing point of a lateral branch, system (8 + 13), camera lucida drawing. The origin of branches of the next degree follows definite lines ; the first leaves of these axes are represented in outline only.
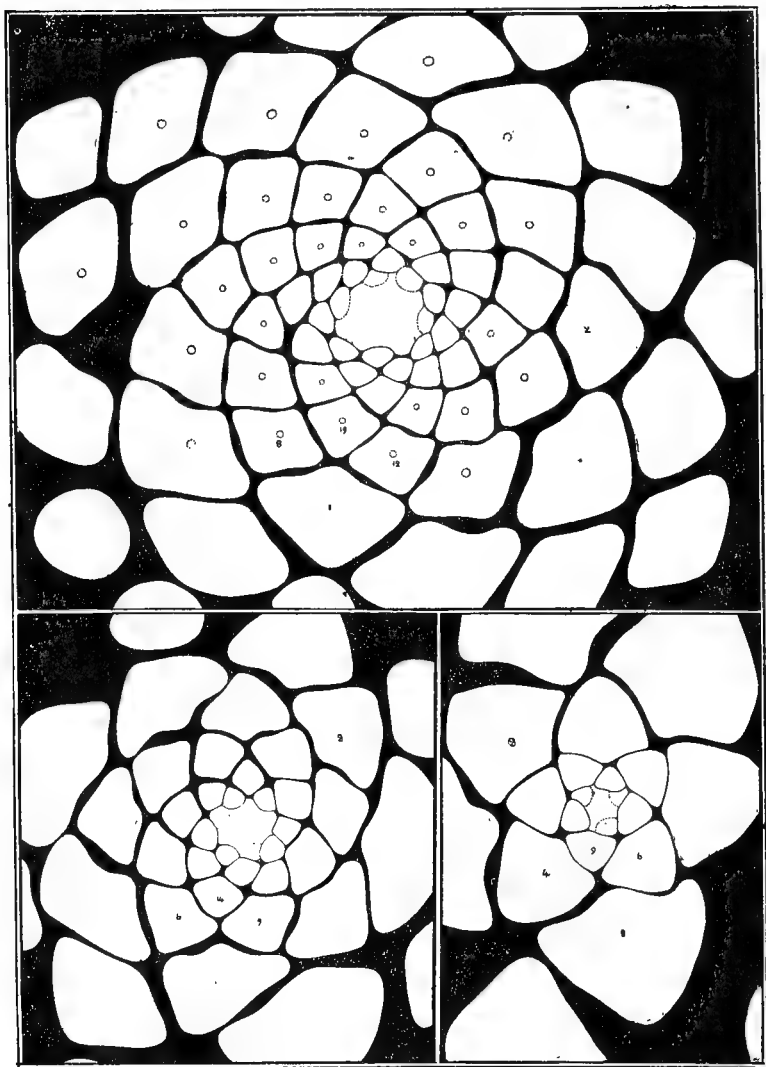
Fig. 41.—*Araucaria excelsa.* Similar sections of successively smaller axes; systems (7 + 11), a branch of the first degree; (5 + 8) a branch of the second degree; (3 + 5) special lateral axis of the third degree.

On drawing sections of such a series of buds under the same lens, with camera lucida, it becomes clear that the leaf-members in all are practically identical, and the leaf-primordium a fairly constant quantity, while the axis is variable.

From the previous table of the curve-systems—

$(8+13)$ corresponds to a bulk-ratio of $5:1$,
$(5+\ 8)$,,   ,,   ,, $3:1$,
$(3+\ 5)$,,   ,,   ,, $2:1$,

respectively; while by drawing a special figure for the system $(7+11)$ it may be shown that the bulk-ratio in such case is very approximately $4:1$ (or $4\cdot2:1$).

From this standpoint, therefore, *Araucaria excelsa* builds its phyllotaxis system according to the relative size of the axis concerned, the ratio being expressed with remarkable accuracy to the nearest whole number, according as the diameter of the axis is 5-, 4-, 3-, or 2- times as large as that of the primordium to be placed on it.

The occurrence of the ratio $(7+11)$ is of especial interest in that it is associated with the normal series, not so much as an exceptional member of another hypothetical series, but definitely as the ratio which gives the missing intermediate bulk-ratio of $4:1$.

Again, comparison of these diagrams shows a striking analogy between the number of primordia of fairly constant bulk placed on axes of different sizes and the segmentation of the tissues of such growing points into constituent cells which also have an approximately equal volume in all. In fact, just as a growing point which is well nourished contains a large number of cell units, and an impoverished one only a relatively small number, so one is bound to conclude, the number of primordia arranged on an apex is an expression of the strength of the growing point.

Whether dealing with cell-segments or lateral primordia, a plant-apex, to use a common metaphor, must cut its coat according to its cloth, and so long as the lateral members remain approximately constant in volume, so the number must vary. In correlation with the relative bulk-ratio of axis and member, a certain number of curves are therefore selected.

Thus a lateral axis which might normally lay down $(8+13)$ curves along which the lateral members would be built owing to a bulk-ratio of $(5:1)$, would if impoverished reduce the number of curves in correlation with the lowering of the bulk-ratio.

Thus $(8+13)$ would reduce simply by dropping out one short curve to $(8+12)$; but the difference in the bulk-ratio thus implied would be very small.* On the other hand, by dropping out one of the long curves, i.e., 8 to 7, it would be necessary to take for the short curves the nearest whole number which gives the same ratio and working-angle; this would be 11, since $8:13::7:11\cdot375$.

The log. spiral construction diagram shows that by so doing the bulk-ratio is lowered to $(4\cdot2):1$.

In the same way, if the long curves were dropped to 6, the nearest number in the required ratio is 10, since $8:13::6:9\cdot75$; and such a change would be correlated with a fall of the bulk-ratio to $(3\cdot8):1$. The next stage of reduction would give as in the normal case $(5+8)$ with the bulk ratio $3:1$.

The systems $(7+11)$ and $(6+10)$ therefore represent approximations to a bulk-ratio $(4:1)$ intermediate between $(5+8)$ and $(8+13)$, and may be expected to occur together with these constructions: thus $(7+11)$ was noted among plants of *Monanthes polyphylla* as equally common with $(5+8)$. In the same way $(6+10)$ occurs commonly in *Pinus (Pinea, pumilio)*, *Podocarpus japonica*, etc., also as an enlargement of a $(5+8)$ system rather than as an im-

---

* The case of such a construction as $(8+12)$ would be of special interest, in that, while it presents no difficulty from the point of view of the loss of one curve from an $(8+13)$ system, the practical result is the immediate formation of a *tetrajugate* system, since $(8+12)=4(2+3)$, and such a system would work out as four concurrent genetic spirals producing four members simultaneously instead of one at a time. The occurrence of such a construction among normal specimens thus either involves a fundamental change in the building-mechanism, or else it implies that the genetic spiral is now comparatively unimportant and only secondary to the curves of the parastichies.

Among a batch of several hundred cones of *Pinus austriaca*, one such cone was found in which a short curve was lost below the widest diameter of the closed cone ; farther up, as in the general case, other curves including long ones were also lost, but the effect of the first loss was, in the case of the dry expanded cone, to render the parastichy system $(8+12)$ as seen on the base, over a considerable area.
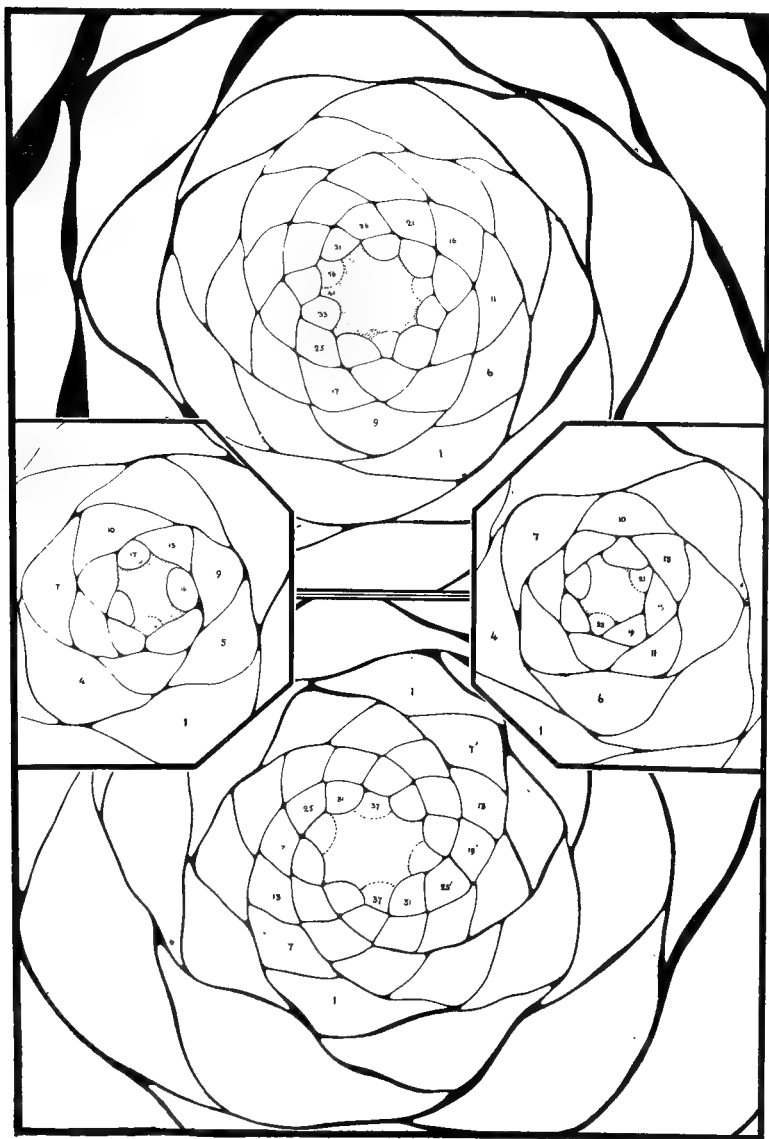
Fig. 42.—*Podocarpus japonica,* Siebold. Sections of leading apices (5 + 8) varying (6 + 10), and weaker axes varying (3 + 5) and (3 + 4).

poverished $(8+13)$; but as $(6+10)$ would constitute a *bijugate* type, it will be considered under the special section. Taken in connection with the approach in these systems to the bulk ratio $(4 : 1)$ which is not provided for in the normal Fibonacci series, special interest attaches to an exceptionally fine closed cone of *Pinus Pinea* in which the parastichies, though somewhat irregular, were for a considerable distance undoubtedly $(7+10)$ (Broome, 1900).

Although thus starting from a standpoint of a *bulk-ratio constant*, it now appears *that the number of parastichy curves becomes of increased practical importance, in that, while the bulk-ratio may be expressed by fractional quantities, the actual ratio of the curves as representing paths of distribution of growth must be expressed by whole numbers.* The very smallest corrections in any system must thus be made in the bulk-ratio, the parastichy curves remaining constant until some very considerable alteration becomes necessary.

That is to say, so long as the plant is condemned by phylogeny to build asymmetrically, one member at a time, and so produce a spiral series, the optimum attempt at symmetrical growth, involving symmetrical nutrition, would be given by the limiting ratio of the Fibonacci series $\dfrac{\sqrt{5}-1}{2}$. In such an ideal system the ratio of the parastichies which map out the orthogonal paths of distribution of growth should therefore be ($\sqrt{5}-1 : 2$); *but as a fractional number of curves is impossible in practice, the nearest approach to this ratio, as expressed in whole numbers, is selected in correlation with the size of the lateral member required.* The number of the curves is therefore more important in practice than a perfect oscillation angle of $137° \ 30' \ 27''\cdot936$. On the other hand,* the approach to the " Ideal Angle" is wonderfully close even in low ratios, being within *one minute* for a $(5+8)$ system.

Constant phyllotaxis may thus be considered from two entirely different points of view ; either a single growth-oscillation producing members with a definite bulk-ratio is the determining cause, and thus involves the fact that so long as one spiral is in operation the numbers of the parastichy curves are only divisible by unity ; or else the parastichy ratios are primary, and being normally successive

* *Cf. Mathematical Notes on Log. Spiral Constructions.*

Fibonacci ratios which have 1 only as a common factor, it becomes possible to draw a single genetic-spiral throughout the entire series.

It will be noticed that the formation of lateral appendages one at a time, which was put forward as being possibly a phylogenetic reason for asymmetrical growth, is not wholly satisfactory ; but if it will not hold, it leaves no clear justification for regarding the tendency of plants, in the more general case, to grow asymmetrically rather than symmetrically, as anything beyond the mere expression of the mathematical fact that symmetrical construction is only to be regarded as a special case of the proposition of growth. This phylogenetic conception was based on the observation that in the great bulk of lower cellular forms, the segmentation of the plant-body into component cells is relatively on so large a scale that it apparently controls the space-form of the entire organism, although it is still possible to regard it as the mere mechanism by which the space-form is divided into units. The range of bulk-variation in the working cells of green plants is remarkably restricted in comparison with the range of bulk-variation in the adult organisms ; and just as in building a small house the size of the bricks may become an important factor, while in a large one it would be negligible, so in the construction of a small plant, histological details are more striking than in immense plant forms. In these simpler constructions, the mechanism of which is apparently controlled by a single apical cell, the practical details of karyo-kinesis and cell-formation require that new members initiated as single cells should be formed one at a time from the initial cell, and it is quite possible to regard this mode of production of a space-form comprised of serially produced members as becoming fixed, and then being retained even after the relative increase in the bulk of the organism and its growth activities would admit of the formation of massive members in which the cell segmentation would be of subsidiary importance. By starting from this first standpoint of a controlling genetic growth movement, which comes into line with the theories of Schimper and Braun, the strength or weakness of the hypothesis should become manifest. It is true that the genetic spiral apparently never reverses, although a

reversal of parastichies may be observed (*cf. Saxifraga umbrosa, Cyperus*); but such phenomena as the transitory variation of an
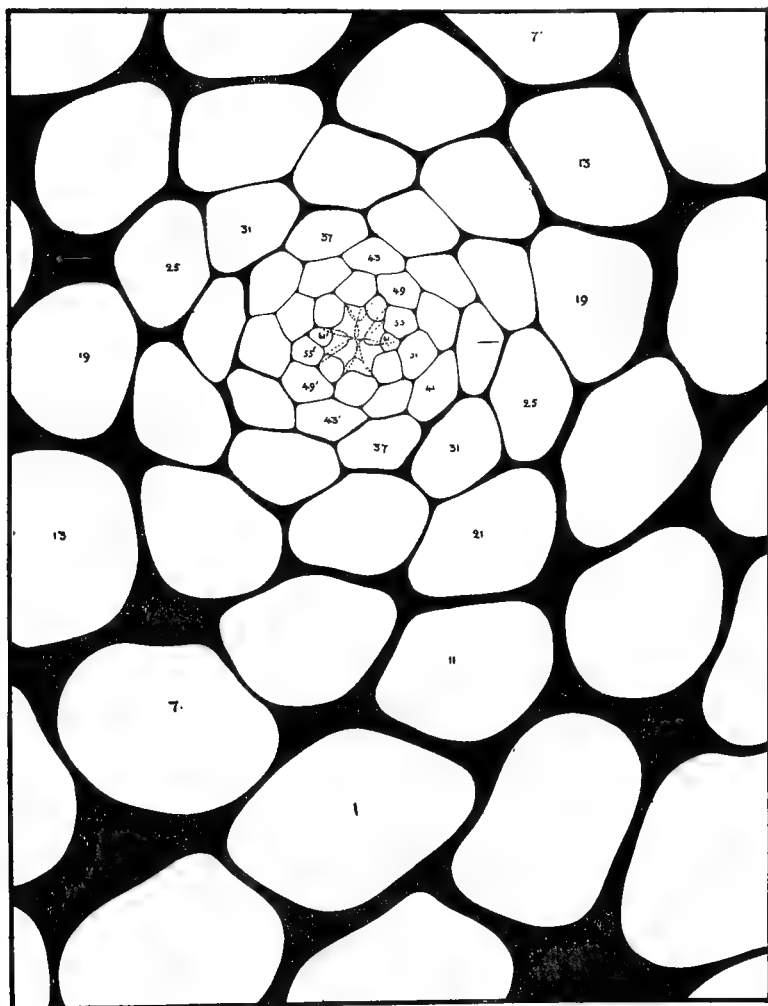
Fig. 43.—*Sedum elegans*, Lej.   Section of shoot-apex (6 + 10).

(8 + 13) Pine-cone to (8 + 12), implying the formation of four genetic-spirals, or the bijugate variation (6 + 10) of a (5 + 8) system

(*Podocarpus*, etc.), become obscured rather than explained; while the assumption of true circular symmetry from a spiral construction is an entirely anomalous proceeding.

On the other hand, the second standpoint, that the parastichies are the controlling feature, certainly gives broader views of the whole range of phyllotaxis phenomena, in that it—

(1) Allows for addition or loss of curves to such an extent that it is immaterial whether the system works out as one or many " genetic spirals."

(2) It suggests a simple transition to true symmetry by equalisation of the number of curves in either direction.

(3) It also presents a clear view of all transitional systems, and especially those included under the term "expansion systems," which will now be considered.

Putting on one side, therefore, any discussion as to what is, after all, to be regarded as the *prime cause* of the asymmetrical growth which thus expresses itself in terms of subjective spirals, it is so far clear that as a matter of practical observation of the phenomena, as well as the discussion and tabulation of the results, this method of regarding the parastichy ratio as being the more immediate controlling factor not only affords more accurate information from a theoretical standpoint, but is even simpler practically than the established method of genetic spiral and so-called "orthostichies" as a means of determining, tabulating, and reproducing the constructions.

III. Rising Phyllotaxis.

As previously indicated, any definite alteration of the system of a constant phyllotaxis must result in a distortion of the parastichy curves. The case of *Dipsacus* in which, with a constant lateral member and varying axis, new members were added or lost to compensate this change in the bulk-ratio, to the very slight extent of losing or adding one or two curved rows, shows that the distortion effect may be considerable (figs. 38*a*, *b*); and it is clear that the same law of adding one member at a time to the system, which controls the asymmetry of the whole construction, must also result in the addition of such compensatory rows one at a time, if the whole system is to change from one curve-ratio to another. If now these changes are initiated on a rapidly expanding apex, such as that presented by the developing capitulum of *Helianthus*, there can evidently be no attainment of symmetry resembling that which previously obtained in the apex, *until every member of the cycle has similarly divided, all round the axis.*

A "Zone of Transition" must thus be intercalated between the two systems, and will form the outward sign of the passage of one system of asymmetry to another with the same approximate curve construction. Previous considerations have further shown that, if the curves remain constant in direction, and the ontogenetic spiral is also constant, change can only take place between alternate members of the ratio series; thus $(5+8)$ rises with a minimum effort and least distortion to $(13+21)$; (*cf.* table in fig. 34).

Confirmation of such a view is very obvious in *Helianthus*, in which the ratio of the contact-curves of the inner sterile involucral scales of the capitulum, bears constantly this relation to the para-

stichy ratio of the disk-florets. (*Cf.* fig. 54*a*, showing the anomalous ratio (11 + 18), the zone of transition being marked by the line of ray-florets, at which the parastichy curves are uniformly increased to form those of the disk-florets (fig. 54*b*).

With these data it is now possible to construct the diagram for any capitulum of *Helianthus*, and to exhibit the relations between the disk-florets and the sterile involucral scales, as well as the position and number of the ray-florets, for any particular phyllotaxis ratio. The compensatory allowances for the inevitable distortion cannot be completely shown, since these are necessarily corrected as the new members are formed, one at a time, and the curve-construction must therefore exhibit the asymmetry of either the former or latter condition. Since secondary changes are very marked in the former system, which produces dorsiventral members only, the curve-system may be constructed from the ratios presented by the parastichies of the disk.

The diagram (fig. 44) is thus drawn for a small capitulum in which the disk-florets have the phyllotaxis (21 + 34), and the inner sterile involucral scales (8 + 13).

By selecting the proper (8 + 13) curves from the (21 + 34) system, it will be seen that the amount of malformation in the diagram is not large.

Since a complete cycle of (8 + 13) contains 21 members, the transition to (21 + 34) will be most economically effected, as already indicated, by an approach to quadrant division in each area; while, to effect the transition, it is necessary to add 13 long curves and 21 short ones. If then one long one and one short are added in each of the first 13 members of the cycle, the last 8 will only require to add one short one each to complete the requisite number.

This is done in the diagram (fig. 44), and the whole construction is closely comparable with the segmentation of a layer of cell-tissue into new lines of cells, as seen in the familiar examples of the cell layer of *Melobesia* or *Coleochaete*. The diagrams here work centripetally instead of centrifugally, but the method of segmentation is identical. Each area is thus seen to be subdivided by two new lines, constituting the new paths in either direction, and these are directly homologous with the characteristic T-shaped wall of

Algal segmentation; the whole thus affording a remarkable confirmation of the original hypothesis, that the formation of massive primordia follows the same laws which control the production of lateral members consisting of single cells. The members which,
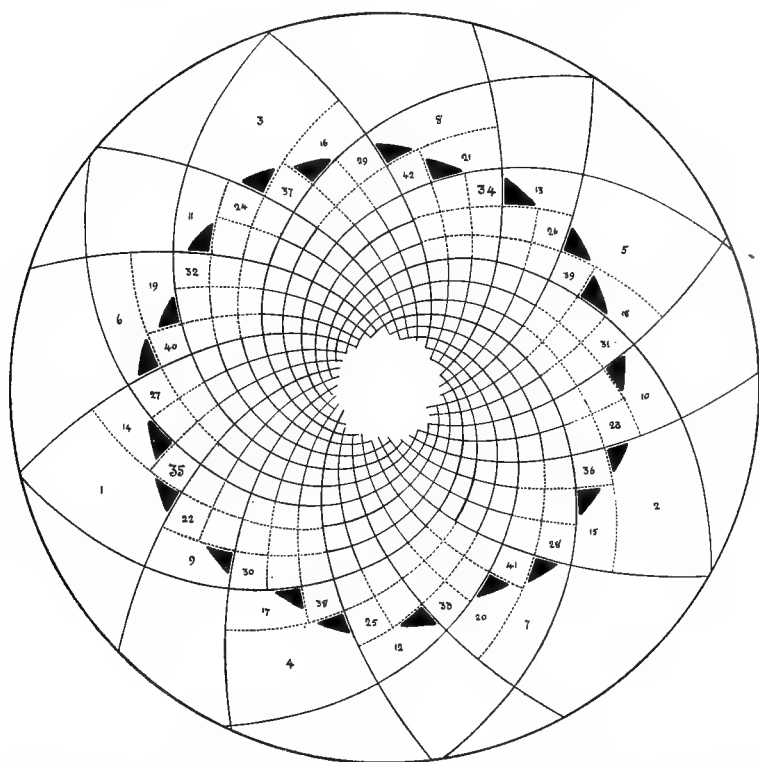
Fig. 44.—Expansion system : log. spiral scheme for the introduction of new paths which determine the rise of phyllotaxis ratios in the capitulum of *Helianthus annuus* from (8+13) to (21+34). A small capitulum is taken as a type ; the genetic spiral winds left ; the small amount of unavoidable error in construction is admitted in the (8+13) system.

in the diagram drawn by this method, exhibit the greatest deviation from "square" areas, are the transitional members which subsequently produce ray-florets. With the view of making the

H

construction clearer, these have been indicated by triangular areas corresponding to their appearance in the capitulum section.

The close agreement of an actual specimen with the preceding
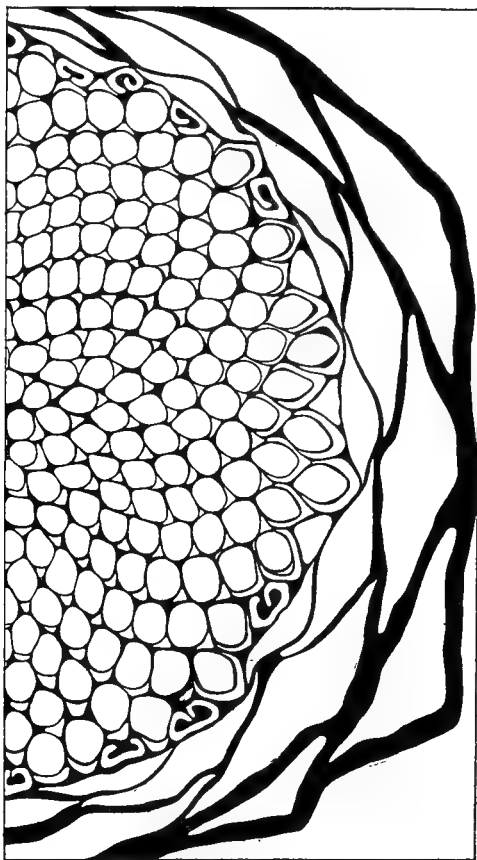
Fig. 45.—*Helianthus annuus.* Section of a young capitulum, 10 mm. in diameter : cam. lucid. drawing of half the disk.

generalisation can be checked on a drawing made from a similar capitulum in the bud stage (fig. 45), and also in the anomalous capitulum (fig. 54).

Fig. 45, drawn under the camera-lucida from a young bud

10 mm. in diameter, shows a very close approximation to such a
theoretical construction. By taking a *curve-tracing* (fig. 46) from
this figure, the agreement becomes much more obvious, and the
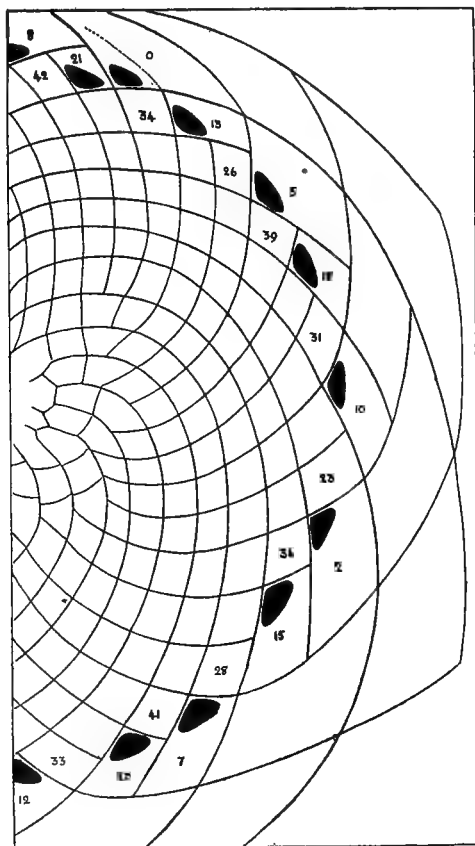
Fig. 46.—Curve-tracing of the preceding ; the ray-florets are blocked in and the
areas numbered in agreement with the theoretical construction of fig. 43.

areas are observed to agree number by number with the theoretical
system. The figure affords a point of additional interest in that
one ray-floret is in excess, and clearly pushed into the circle of
rays out of its place. Comparison of the numbered tracing shows

that this belongs to member 0, and represents a case of the fertility of the last involucral member. The fact that the number of sterile ray-florets is not absolutely constant is thus illustrated, while it may be noted that such irregularities will also affect the observed number of involucral scales as a constant quantity.

Deviations from theoretical construction are seen to be due merely to:—(1) The assumption of dorsiventral symmetry by the sterile involucral scales, which further exhibit sliding growth over one another in the tangential direction to such an extent that a ray-floret is sometimes isolated from its subtending bract, while the members themselves are greatly flattened radially. (2) Owing to the sharp line of demarcation between these dorsiventral members and the fertile bracts, which with their enclosed radially-symmetrical florets retain their original relative volume, the edge of the disk becomes a fairly rigid circular boundary against which the decadent ray-florets are subsequently pressed. The ultimate assumption by these latter of a form adjusted to the room allotted them in the bud is thus not due to the fact that they are subtended by members of transition; while since the same influences may act to a greater or less extent in other peripheral florets, the number of ray-florets is not absolutely constant, although the approximation to the theoretical number is very close.*

Transition to a higher scale of phyllotaxis, on an axis which is rapidly expanding without correlated expansion in the lateral members, thus takes place in alternate stages of the ratio series.

Thus in the specimen of *Cynara Scolymus* figured, the large involucral scales (figs. 9, 52) showed on the sides of the capitulum the obvious parastichies $(8+13)$, and these are further seen to be contact parastichies in section of the head. After production of 79 of these the phyllotaxis rose to $(21+34)$ and 102 smaller sterile scales were laid down, while at the edge of the disk the phyllotaxis rises to $(55+89)$, with which curve-construction the disk-florets are produced without subtending bracts (fig. 52).

The total number of sterile scales (181) being relatively large, and greater than the number of florets in one complete cycle (144),

---

* *Cf.* Weisse, *Variation Curves*, p. 480, tables; Ludwig, Ueber Variations-kurven, *Bot. Centralb.*, lxiv. p. 102.

shows that the involucral region is here much more developed than in *Helianthus*, while two complete transitions are included in the construction.

The relation of two such transitional systems to one another therefore remains to be considered.   Does the transition take place rapidly and with a minimum number of members, or is it irregular and spread over a large number?   In *Cynara* the number of members observed is very large, and in absence of further data either method may be possible ; the remarkable accuracy with which the transition has been planned for *Helianthus* suggests that the latter plant may be taken as a type.

Before passing on to the case of the double transition, the mechanism of the normal expansion of *Helianthus* capitulum requires to be carefully considered.   As already noted, such a transitional system presents the appearance of a cell-segmentation, or even a process by means of which primordia are as it were separated out along specially formed lines of cleavage.   The whole construction is influenced rather by the preceding parastichy lines than by a definite genetic spiral, and the system grows throughout along its pre-established paths of asymmetry.   This agrees with the facts observed in the actual ontogeny, so many new members being formed simultaneously that the genetic spiral is hopelessly lost sight of, and can only be traced by numbering the members.

It would appear now that the genetic spiral as a line of building has lost its significance ; the question of phyllotaxis becomes one of continuing an expansive development along similar curved paths, and the plant continues to work out a definite pattern quite mechanically.

It is clear that while such expansion may be pursued indefinitely, the same ratio system will always be constantly maintained, and constructions in the very highest terms of the Fibonacci series thus become conceivable, not by accuracy of the building-mechanism however, which in such case would come down to a question of working at an angle correct to minutes and seconds, but by simply following up a system of construction which maintains at all stages an approximately identical degree of symmetry.

The method of employing this expanding mechanism may now

be considered, the process being rendered obvious by the fact that the ray-florets in the case of the Sunflower occupy the transitional areas between two cycles.

Comparison of the figure in which 21 ray-florets are indicated as black patches shows that these follow a remarkable sequence which, counting from No. 1 in the direction of the genetic spiral, may be represented by the figures—

$$2 \cdot 1 \cdot 2 \cdot 1 \cdot 2 \mid 2 \cdot 1 \cdot 2 \cdot 1 \cdot 2 \mid 2 \cdot 1 \cdot 2$$

The fact is thus brought out that the essence of the Fibonacci series consists in the manner in which it may be regarded as composed of the expression $2 + 1 + 2 + 1 + 2$ treated as a recurring quantity. Thus 3 of these members add up to 5, 5 to 8, 8 to 13, any 13 to 21, and any 21 to 34, etc. Any ratio of the series may undergo subdivision in this sense to produce the next higher member. From this it follows that the law of arranging members of a higher cycle on a preceding lower one consists in the method of dividing them in sequence in the order indicated. And *conversely*, whenever increase of members takes place in such a manner, it is at once clear that a transitional sequence of the Fibonacci series is implied (*cf.* Cactaceae).

To subdivide a phyllotaxis system so as to retain the Fibonacci ratio, it is therefore only necessary to start from No. 1, in the direction of the genetic spiral, and put in new paths in the sequence $(2 \cdot 1 \cdot 2 \cdot 1 \cdot 2)$, or graphically—

I.   .   . $\mid$V I V I V$\mid$V I V I V$\mid$, etc.

When two such transitions are involved, the sequence becomes $(3 \cdot 2 \cdot 3 \cdot 2 \cdot 3)$, or—

II.   .   . $\mid \begin{matrix} V & V & V & V & V \\ V & I & V & I & V \end{matrix} \mid$, etc.

By noting this property, the $(8 + 13)$ curves are selected from the $(21 + 34)$ set, the sequence being carried out along the direction of the spiral concerned; thus in the practical construction of diagrams, it is necessary to start from 1 and proceed from the concave side of

the curve, marking out sections of $(3 \cdot 2 \cdot 3 \cdot 2 \cdot 3)$, etc., all round the system (fig. 44).

The same relation will be found to hold for other ratio-systems. Formula II. thus gives a special case of the law of subdivision of paths of growth, corresponding to the $\top$-shaped segmentation of Algal membranes; while the graphic method of representation furnishes a key to the construction of a normal transition system. Deviations from it will imply irregularity in expanding phyllotaxis; while a guide is again provided for checking the anomalous addition of new ridges as a consequence of the formation of new parastichies in many Cactaceae.

The areas on such a construction diagram are readily numbered, the members of the original $(8+13)$ system being marked out by their differences of 8 and 13. Although the diagram was constructed empirically to begin with, the correspondence of such a theoretical construction with the phenomena actually observed in a capitulum (fig. 45) is so striking that the accuracy of the method is beyond doubt, and its mechanism may be further analysed. Thus, the system was originally $(8+13)$; each of the first 13 new members adds a new long curve and the system is thus gradually changed to $(21+13)$.

It is important to note that when forking of the paths takes place, it is the external or peripheral portion of the subdivided segment which must always be regarded as the "member adding the new curve."

Thus 1–13 each adds a new long curve in 13 segments of the original $(8+13)$ system.

The system is now practically $(21+13)$, which, it must be noted, is quite a different construction from $(13+21)$, although the possibility of an adjustment on the part of the plant is not to be neglected, since the transition takes place in a growing system.

No. 14 again adds the first short curve; 21 of the same type are required, and thus 33 adds the last one of the set, and at 34 the new system is completed, and the Fibonacci ratio is again perfected and may be continued indefinitely. But if expansion is to again commence, it is clear that it cannot begin before the 34th member. *In a normal system, therefore, each member adds one new path to the*

system ; the difference in the number of curves between two transition stages gives the number of members involved in the change, thus :—

$$(3+5) \text{ passes into } (\ 8+13) \text{ in 13 members.}$$
$$(5+8) \quad ,, \quad (13+21) \text{ in 21} \quad ,,$$
$$(8+13) \quad ,, \quad (21+34) \text{ in 34} \quad ,, \quad \text{etc., etc.}$$

The law of normal expansion is so simple, and works in *Helianthus* capitulum with such remarkable accuracy, that there can be little doubt that it represents in some way a mechanical distribution of growth-energy which is a common property of all plants growing under conditions in which these mechanical relations are allowed free scope.

As soon as the Fibonacci ratio is disturbed, the system gradually and uniformly proceeds, one member at a time, to put it right again. The addition of all the long curves before the short curves are put in is perhaps the most curious feature. It may be also noted that though the initiation of the change makes for symmetry, by raising the lower number of the ratio first, the ratio is equalised, then again rendered unequal, and again equalised at one point in putting in the short paths; but the system does not remain stationary at these points of symmetry, it passes on and only rests in the condition of equilibrium of the completed ratio. Although the acquisition of a Fibonacci ratio may be regarded as the optimum attempt at symmetry in an asymmetrical system, the plant does not so far show any preference for a symmetrical relation attained during a period of transition. Nor is it clear that such a point of symmetry, although isolated in the construction by considering one new curve at a time, is at all comparable with a true symmetrical construction. The whole system is growing together in a correlated method, and the metaphor of crystallisation is perhaps the only one which fits the phenomena observed.

Now that the number of members involved in making any given normal expansion is known, it remains to see to what extent one expansion can rapidly succeed another. Thus in the *Helianthus* capitulum taken as a type, it appeared that a new system could only commence at the 34th member or beyond it. The data given for *Cynara* show that the number of members of each system was

considerably in excess of the theoretical minimum, and the conclusion is warranted that the expansions may take place at intervals at irregular distances from one another, although the actual transition may be limited to the minimum number of members; the new ratio being continued for an indefinite number of members before a new change takes place.

Thus the Daisy (fig. 47) shows a double transition, from $(2+3)$ foliage leaves, $(5+8)$ involucre, to $(13+21)$ florets. The ends of the system are not obtainable, but it is obvious that 13 involucral members of the $(5+8)$ system are retained when the complete transition would have been completed in 8.

Very remarkable relations occur in *Helianthus* in the number of members constituting the involucre, and the tendency of *Helianthus* to approximate a continuous expanding system is very marked. Thus the involucre of a $(55+89)$ capitulum should contain 34 sterile scales; the range (Weisse) is $26-42$, but it must be borne in mind that the exact localisation of the involucral region is a matter of difficulty, since the reason which determines which scales shall be the first to produce florets is not known, and the range is thus as equally open to minor variations as the number of the ray-florets themselves. The variation curves tabulated by Weisse show that similar ratios hold for capitula exhibiting the other parastichy systems on the disk, and the number of sterile involucral scales is thus one grade lower along the ratio series 3, 5, 8, etc., than the theoretical number of ray-florets. The involucre of *Helianthus* thus apparently includes the whole of the members involved in one complete transition, while a second transition takes place immediately after, of which the ray-florets represent those transitional members which have to negotiate the bulk change. Since the head taken as a type in fig. 45 is only of a low order $(21+34)$, and the involucre therefore $(8+13)$, it would follow that some of the foliage leaves were laid down with a $(3+5)$.

But much larger heads are found, so that it becomes probable that more than two such transitions may take place in such a rapidly expanding axis.

It has already been shown, for example, that *Cynara* shows two transitions in the involucre, and another at the edge of the disk:
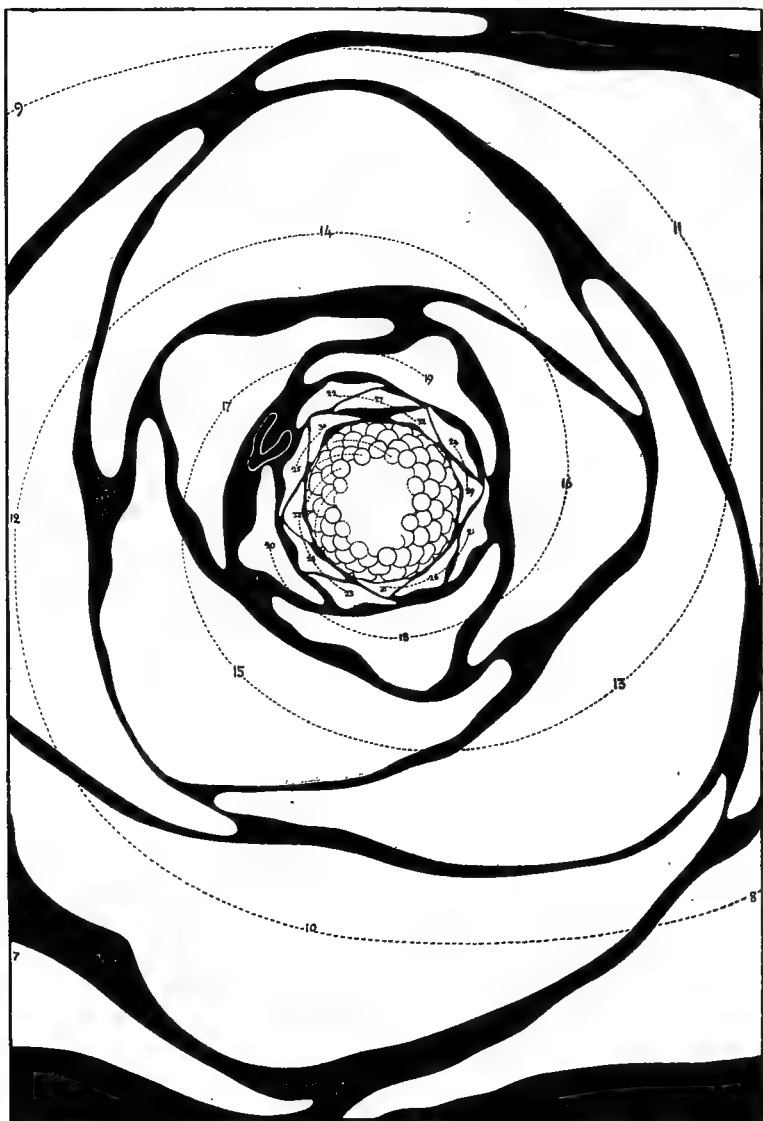
Fig. 47.—Transverse section of the whole central portion of a perennating plant of *Bellis perennis* (January), showing expansion systems (2+3), (5+8), and (13+21): cam. lucid. drawing.

the disk being $(55+89)$, inner involucre $(21+34)$, outer involucre $(8+13)$, and the upper foliage leaves $(3+5)$.

Comparison of the Daisy (fig. 47) again shows foliage leaves $(2+3)$, involucre of 13 members $(5+8)$, and florets $(13+21)$, the rays being not yet determinable.

A large $(89+144)$ Sunflower would therefore be built up by the regular expansion $(2+3)$, $(5+8)$, $(13+21)$ foliage leaves, $(34+55)$ involucre, and $(89+144)$ florets of the disk, thus giving five complete transitions along the axis. The difficulty of giving a definite phyllotaxis constant for the leafy stem is thus rendered obvious.

It now becomes possible to give a connected account of the phyllotaxis phenomena of *Helianthus*, based on this remarkable limitation of the involucre to the minimum number of members which represents the transitional period between two cycles, and the following scheme is borne out by the data tabulated in the Variation Curves of Weisse (*loc. cit.*, p. 478). The weakest Sunflower axis resembles the Daisy in presenting two changes only : *i.e.*, beyond the 3–4 pairs of decussating $(2+2)$ leaves of the seedling, the system assumes normal asymmetry by laying down $(2+3)$ curves. After producing a total average of 20–22 foliage leaves (average of 20 plants $=22$), the system expands to $(5+8)$; since 8 new curves are to be added, 8 members represent the minimum number of leaves before another transition can be initiated. Such an involucre would therefore normally contain 8 leaves and the second transition would give $(13+21)$ florets system, of which the first 13 would form the ray-florets.

If, for example, after forming 8 members of the transition to $(5+8)$ the vegetative condition was still vigorous, a further rise to $(13+21)$ would be effected in 21 leaves, the involucre would now be 21, the total number of leaves about $22+8=30$, and the parastichies of the disk $(34+55)$ (Weisse, p. 478). Again, with the same proviso another change in the vegetative region to $(34+55)$ would be effected in 55 leaves, and if these represent the involucre the next rise $(89+144)$ would give the largest capitulum. Such a plant should show $(22+8+21)=51$ foliage leaves and 55 involucral scales, total 106. It is of interest to note that one such plant counted by Weisse gave 46 of the former and 62 of the latter, total 108 ; when allowance is made for the ill-defined character of the involucral region, the correspondence is remarkably close.

That *Helianthus* presents a progressively rising phyllotaxis involving the minimum number of members with a remarkable degree of accuracy appears therefore fairly clear. Similarly $(3+5)$ as a stronger system would give other terms of the capitulum series, and expanding systems derived from variation derivatives $(2+4)$, $(3+4)$, would lead on to capitula of the series 16, 26, 42, 68, and 29, 47, 76 respectively. These variations are however comparatively rare, the former representing the

bijugate capitula described, and the latter including all the anomalous constructions yet observed. On the other hand, while it is probable that such generalisations represent the *general tendency* of the phyllotaxis phenomena in *Helianthus* with a considerable amount of accuracy, it is not necessary to assume that they will give absolutely accurate results in the case of individuals. Examination of the apices of a large number of young plants is sufficient to show the possibility of a considerable amount of variation, the causes of which are still unknown.

The agreement of the preceding data with the observations of Weisse shows that even if continuous expansion does not take place, a margin of about twenty leaves suffices to cover all the members formed in any Sunflower plant which do not belong to such a construction, including the first leaves of the seedling and odd members filling the gaps between transitional systems.

These generalisations require therefore to be tested on actual apices in which the transition is being effected. The difficulty of the method will lie in the fact that only one section is obtainable from any given plant, and there is thus no telling what the system observed would have passed on to if the plant had been left alone until the capitulum was reached.

Owing however to the remarkable uniformity of growth in the bud of *Helianthus*, it is possible to cut sections which practically include the whole of the phyllotaxis system so far as it has gone.

The first and most remarkable aberration observed in the Sunflower is that the apex commences in the plumule a definitely symmetrical construction, and changes to normal symmetry at a subsequent and varying date.

Thus seedlings which have not as yet produced their first leaves beyond the green cotyledons, show on sectioning two or three pairs of decussating leaves constituting the terminal bud of the plumule and contained in the cotyledon tube (fig. 48*a*, three pairs).

Asymmetry may commence early ; at the 5th leaf while still enclosed in the tube (fig. 48*b*), or it may be delayed until the first leaves are well grown.

Seedlings in which two pairs of leaves are well developed on the elongating axis should afford suitable material for the onset of asymmetry. In such buds most usually the $(2+3)$ system is directly assumed (fig. 48*d*, for 10 leaves), more rarely symmetry
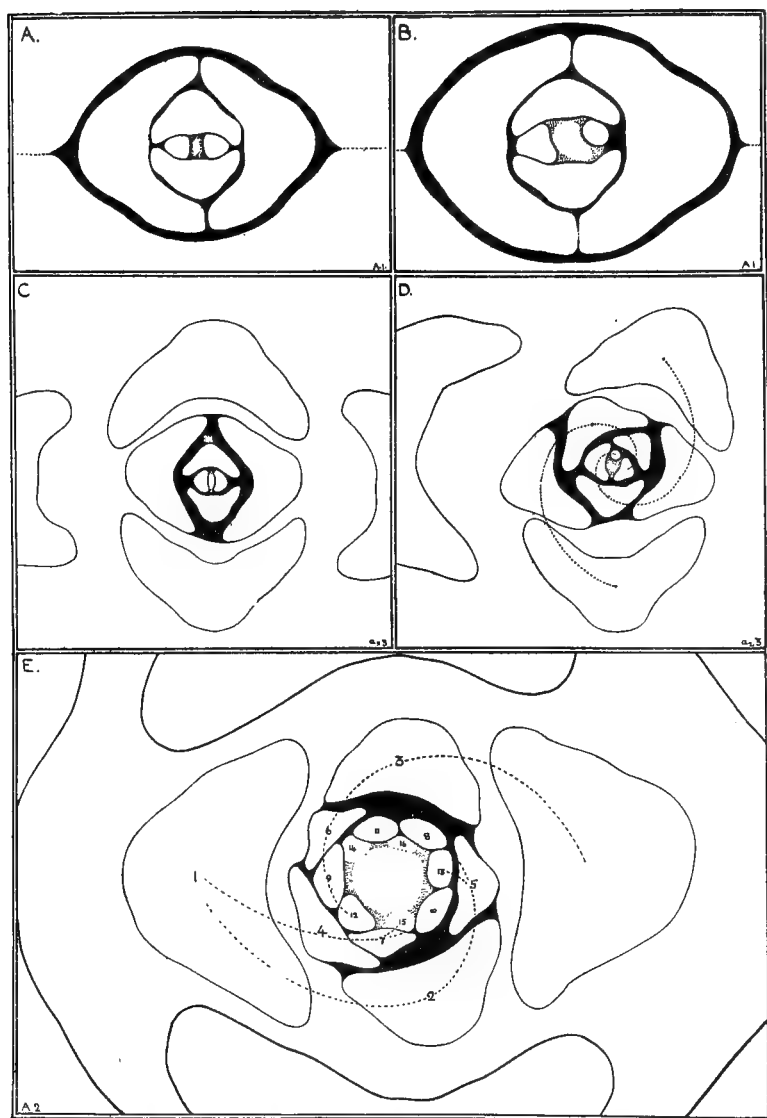
Fig. 48.—Apices of seedlings of *Helianthus annuus*, cam. lucid. drawings. A and B, cotyledons only showing ; A, symmetry for three pairs of leaves ; B, commencement of asymmetry at the 5th leaf; C, older seedling, symmetry maintained for 5 pairs ; D, asymmetry (2 + 3) above a symmetrical pair ; E, asymmetry (3 + 5) following a decussate series and already changing at 8 to a higher series.

may be continued (fig. 48*c*, five pairs), and in other cases the $(3+5)$ system may be produced directly beyond the decussating members (fig. 48*e*). This last example is of interest in that the $(3+5)$ system immediately commences a further rise, and examination of the method shows that the leaf numbered 8 is the first member definitely concerned, in that it does not fall accurately between 3 and 5, in the manner that 7 fell between 4 and 2, but beyond its normal station, so that 13 afterwards falls behind it, in the manner tabulated in fig. 44 as the type expansion.

Another example (fig. 49) shows a similar transition only taking place after a formation of 13 members of the asymmetrical system (Nos. 14 and 19 falling in the gap between 9 and 11). The fact that older leaves in *Helianthus* are spaced out owing to a great development of hairs, militates against accurate observation of the contact lines in sections of large area, but by remembering that each leaf fills its own rhomb, and that the development of hairs thus compensates the diminution in the rate of growth of the leaf itself, the contact-lines of the hairs of adjacent leaves may be taken as a very approximate representation of the theoretical members.

Since the sudden change from a decussate $(2+2)$ to an asymmetrical $(3+5)$, implying the sudden intercalation of four new curves, is much less easy to understand than the change to $(2+3)$ which only adds one, a capitulum of $(21+34)$, similar to the one for which a diagram has already been constructed, may be selected, in that it should present a double expansion of the type $(3+5)$, $(8+13)$, $(21+34)$.

Such a capitulum in the bud condition, the whole 6 mm. in diameter, is sectioned in fig. 50; every member being accounted for beyond the uppermost pair of decussating leaves.

As a $(21+34)$ capitulum should present 21 ray-florets, 13 involucral scales, and an average of 25 foliage leaves, including the primary decussating pairs (Weisse), the bud in question is evidently well within normal range in that it shows a total of 27 vegetative members between the uppermost pair and the first ray-floret. By adding 8 for an average number of four pairs, the total number of leaves should have been 35, which is again sufficiently close to the theoretical number $25+13=38$; the specimen is thus a normal

plant so far as it goes, and well within the range of the Variation
Curves.   Again, in the system $(3+5)$, $(8+13)$, $(21+34)$, the
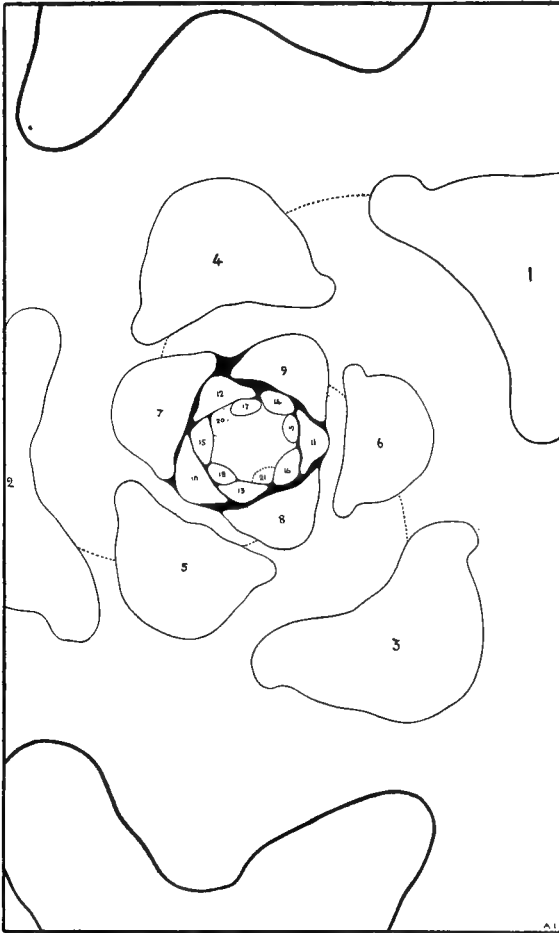
Fig. 49.—Seedling of *Helianthus annuus*, $(2+3)$ system above decussating leaves :
transition to a higher series after asymmetrical production of 13 members.

members along the long curves differ by 3, 8, or 21 respectively,
and since in dorsiventral constructions the long curves are more

obvious than the shorter ones, these paths may be studied as a whole and mapped out by curved lines passing through the members differing by these values, and the method of the forking of the long curves of the system made more obvious (fig. 50). The method of numbering may be checked by noting the proper differences in adjacent members, and also by taking an approximate divergence angle of 137°.

Bearing in mind the convention previously laid down in the type capitulum of fig. 44, that the member which originates a new curve is always the external member of the two paths produced by the forking, the system may be further analysed.

Starting from the uppermost pair of decussate leaves 1 and 2, No. 3 commences the asymmetrical condition and adds a new curve; three long curves are now established and the original $(2+2)$ system completes the transition to $(3+5)$ in the members 3, 4 and 5.

Normal expansion commences immediately in 6, since 6 is the external member of the fork $3\Big\langle\begin{smallmatrix}6\\11.\end{smallmatrix}$

Thus 6 puts in the first new long curve, and similar relations hold for 7, 8, 9, and 10. Five long curves are now added, and the system is at this moment $(8+5)$. As in the normal case, the short curves immediately commence to be laid down, commencing at 11, which is the internal member of the previous fork, but the external member of the branch $6\Big\langle\begin{smallmatrix}11\text{ (difference of 5)}\\19\text{ (\quad ,, \quad 13).}\end{smallmatrix}$

Similar relations are established for the members 11–18 inclusive, and 19 adds no curve, being the inside member of the last forking, and falls in the gap left for it. No change takes place till 30 is reached; that is to say, 20 to 29 inclusive, or 10 leaves are formed in a uniform $(8+13)$ system. At 30, however, a long·curve is again added, since 30 is the outside member of the fork

$$22\Big\langle\begin{smallmatrix}30\text{ (difference of 8)}\\43\text{ (\quad ,, \quad 21):}\end{smallmatrix}$$

as the first member of the ultimate transition, it also correctly subtends a ray-floret. Similar relations hold for 30–42 inclusive,
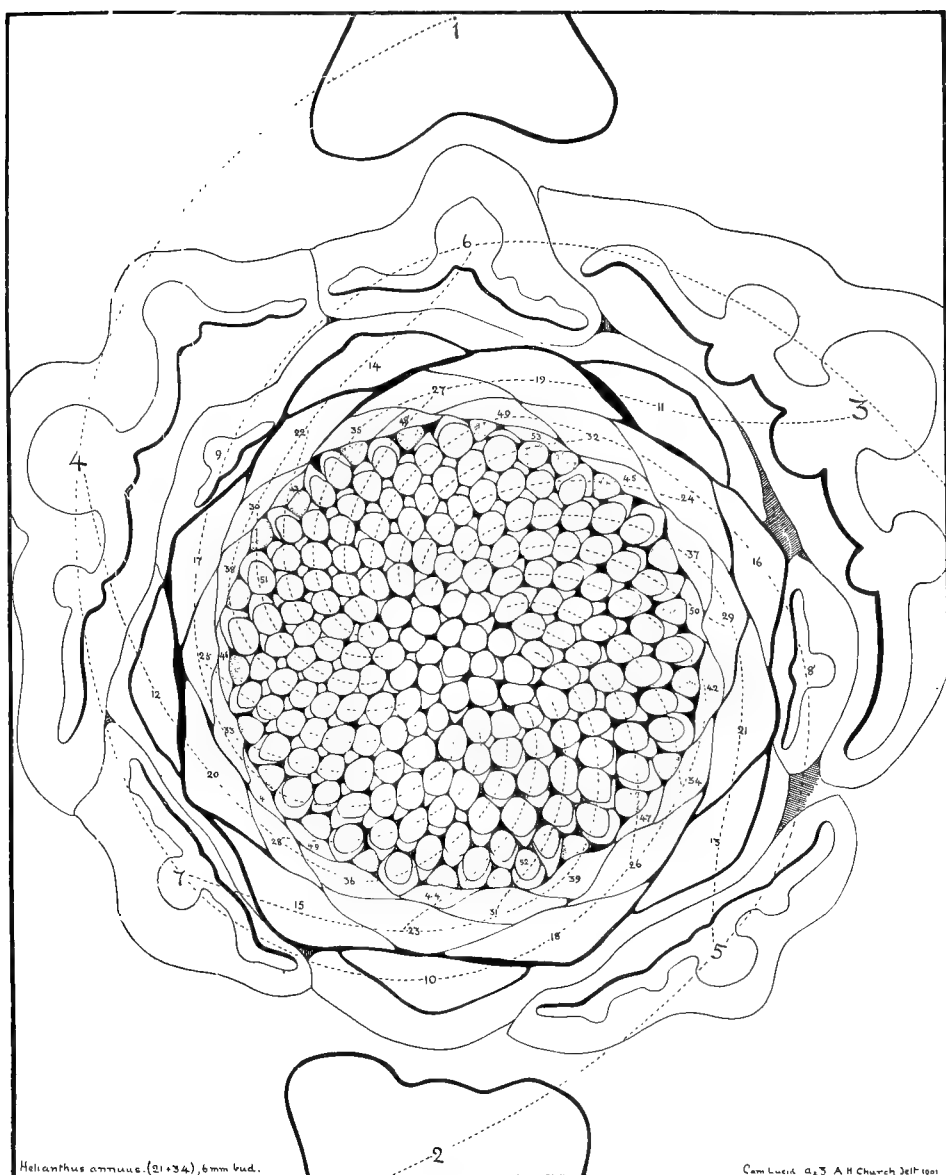
FIG. 50.—*Helianthus annuus.* 6 mm. bud of a (21+34) capitulum : cam. lucid. drawing of the whole plant, in a transverse section, beyond the uppermost pair of decussate leaves. Two complete expansion systems (3+5), (8+13), (21+34) are included : the more obvious paths of the longer construction curves are dotted, and the introduction of new paths rendered clearer.

or the 13 members required to add the long curves of the system now momentarily (21+13). At 43 (the internal member of the 22 fork), a short curve is added and 21 new short ones are put in between 43 and 63, the system being completed at 64. This latter change may be better checked on a construction diagram similar to that of fig. 44, in which No. 1 is replaced by 30. The correspondence is again exact, and the actual construction of the diagram and the addition of the new curves one at a time, as they are observed on the specimen, is required to fully comprehend the symmetrical relations of the construction. The ray-florets, it will be noted, should extend from 30–50 inclusive; a minor variation is of interest in that in this specimen an extra ray-floret, since 22 are actually present, is formed from a disk-member, while in the previous capitulum of fig. 44 an extra one was produced by an involucral member. Thus the floret in the axil of 53 forms a ray, and the member flattens out to an involucral scale, while 51, 52, and 54 are normal disk-florets.

The identity of the expansion mechanism, which is thus twice repeated in one section, with the construction previously postulated is very striking, and nothing is more remarkable than this *rhythmic interchange* in the addition of the curves in the two directions.

It will be noted that in the case of the production of (3+5) from (2+2) the transition was very rapid, and not conformable to the rule for asymmetrical expansion unless the decussate condition be regarded as a variation of (1+2), in which case expansion should be completed in 5 members. In such case the next expansion commences immediately at 6, while a wide gap separated (8+13) transition from the (21+34), 10 members being laid down with constant phyllotaxis. The previous estimates for the phyllotaxis phenomena of *Helianthus* are thus subject to an error of a variable number of members between the systems, and the involucre does not necessarily include a definite transitional period. The limitation of the involucre of *Helianthus* to a minimum number of leaves has nothing to do with the expansion mechanism, but represents that number of members which makes a complete cycle of contact around the axis before the last transition commences at the region of ray-florets. *Helianthus* may then be taken as a

I

type of plant in which very considerable expansive changes take place, and the optimum succession of the transitions may be very closely approximated.

That such perfection of transition is not the general rule is seen in *Cynara*, in which a change was only effected after a considerable number of members of the different system had been laid down. The case of the Daisy is also of interest, in that 13 involucral members are retained in a capitulum which would in *Helianthus* average 8; this involucre of 13 being practically constant for the Daisy (Ludwig).*

Again, the essential feature of such transitions lies in the fact that, given a ratio of the Fibonacci series, the change is rapid, and when completed gives another member of the Fibonacci system. From this point of view, the ratios of the Fibonacci series may be regarded as stations of stable equilibrium, in that they give the optimum working angle and set of curves plotting the system, and any alteration of such a system produces a state of instability which as rapidly as possible resumes the Fibonacci relationship. The changes may take place with the minimum number of members intervening (*Helianthus*), or they may be separated by a larger or even variable number (*Bellis, Cynara*); but the change when it does take place is in these types rapidly negotiated and the "stable equilibrium" of a Fibonacci ratio regained.

So long, therefore, as it is regarded as a mere *convention*, which describes phenomena without explaining them, it is convenient to regard a normal plant as possessed of what may be termed a *Fibonacci sense*, by which any alteration in the phyllotaxis system, whether due to alterations in the bulk-ratio or not, is controlled and corrected to a system of the normal optimum series.

In other plants, there may be no evidence of any such controlling power: examples being afforded by the stems of tree-ferns and

* The relation between these constructions may be obtained from the contact relations of dorsiventral members. It consists in the fact that while 8 members of a $(5+8)$ system form a minimum single investment to an axis, 13 will form a double one. The limitation of the calyx of a pentamerous flower to 5 members of a $(3+5)$ system is thus curiously repeated in the case of the similarly protective involucre of the Sunflower capitulum.

Cactaceae. As an extreme case a specimen of *Cephalocereus senilis* may be cited, in which new curves were added singly, and without rule, at intervals of about 700 leaves.

While, however, each normal expanding system presents the appearance of growing out of its predecessor so that the curve ratio remains and will thus remain practically constant, the point of view of bulk-ratio becomes lost. An expanding type may represent, as in *Helianthus*, a fairly constant bulk-ratio affected by an expanding axis, and this as a special case may be separated from types in which the bulk-ratio is the only variable quantity. That such may occur is shown by the rising phyllotaxis of such inflorescences as those of *Dipsacus*, in which very small florets occur almost immediately after large "decussate" foliage leaves on an axis which does not continuously dilate; and in the same way the members of a flower may be laid down with a varying bulk-ratio on either a constant or a variable axis. In such case, if the change of ratio is sufficiently large, it is evident that given a constant genetic-spiral, the direction of the parastichies may remain unaffected as in the preceding example of normal expansion.

The possibility is, however, not eliminated that the change in bulk-ratio may not be correlated with the previous system, and that a definite break in the phyllotaxis will thus be produced. With the same genetic spiral, that is to say, the bulk-ratio may be so independently affected that the parastichies will reverse and the system show more obvious distortion.

Such systems may be included under the term DISCONTINUOUS PHYLLOTAXIS, and will be characterised by a reversal of the contact-parastichies.

Two examples of such phenomena may be considered.

I. *Cyperus alternifolius*. The strap-shaped foliage leaves are produced in a $(1+2)$ system giving three spiral series (spires) (fig. 59b), which owing to the approximate equality in radial depth of the developing members become approximate spirals of Archimedes, without necessarily implying any torsion phenomena; but beyond these biologically specialised members, small unmodified scale leaves subtend the spikelets of the terminal cluster (fig. 51). These
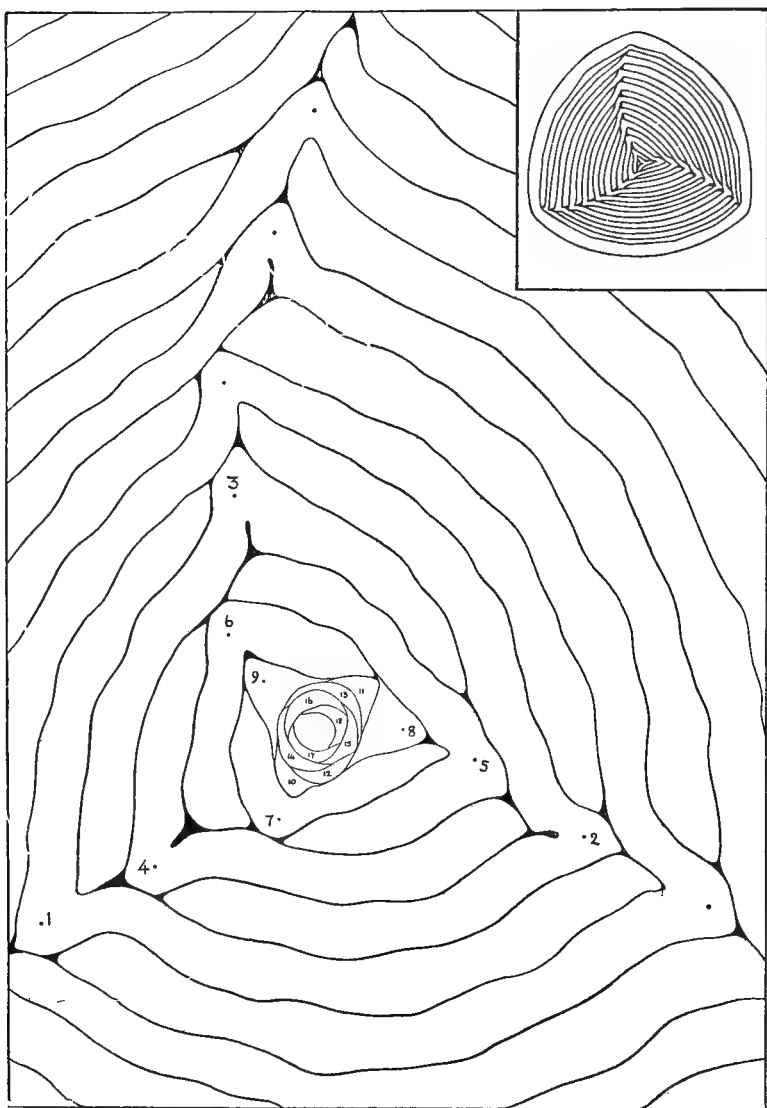
Fig. 51.—*Cyperus alternifolius*, R. Br.   Section of shoot-apex (November), three-spired system $= (1 + 2)$, enclosing terminal system of scale-leaves $(2 + 3)$.   Left-hand spiral apparently broken at No. 12.

present a phyllotaxis $(2+3)$ which is evidently correlated with the assumption of a lower bulk-ratio. The transition is abrupt, and takes place at the member numbered 12, which is thrown forward to such an extent, that the genetic spiral at first appears to have been reversed; the new curve established at this point allows No. 14 to fill in the gap behind 12. The parastichies are reversed and a very definite distortion of the system is apparent at the junction of the two systems.

II. *Saxifraga umbrosa* (London Pride). Young shoots produce leaves in a rosette of the type $(2+3)$, older ones may exhibit $(3+5)$. Sections of a bud taken in January show the new year's growth already laid down within the rosette of the previous season and already terminated by a developing inflorescence. In such cases a break occurs at the junction of the two seasons' growth (fig. 52). This is exaggerated, owing to the fact that the last formed leaves of the previous season were poorly developed and never attained adult form (11 and 12). The same break in the genetic spiral, and reversal of the parastichy curves, is observable : the genetic spiral continues in a right-hand direction, but the long curves are now differing by 3, the short by 5 ; the dislocation of the junction is shown by the curious relations of the members numbered (along the curves) 13 and 15 ; and this, taken into connection with the rudimentary condition of 11 and 12, militates against any view that the $(2+3)$ appearance of the older members is merely an effect of sliding growth due to the formation of a sheathing leaf-base.

These two examples suffice to show—

(1) A new system may be originated at a new period of growth producing similar members on a presumably increased axis.

(2) That on a constant axis the bulk-ratio may be lowered so as to admit of a system which has no direct relation in the distribution of its curves to the previous construction.

The latter case is of great importance in dealing with the insertion of floral members in floral structures, while the former

is of special interest in connection with renewed growths. Both phenomena again may be involved in the general rise of phyllotaxis observed in young plants which develop mature axes with a comparatively high ratio of curves.

Thus it is clear that the youngest plants of *Aspidium Filix-Mas*,*
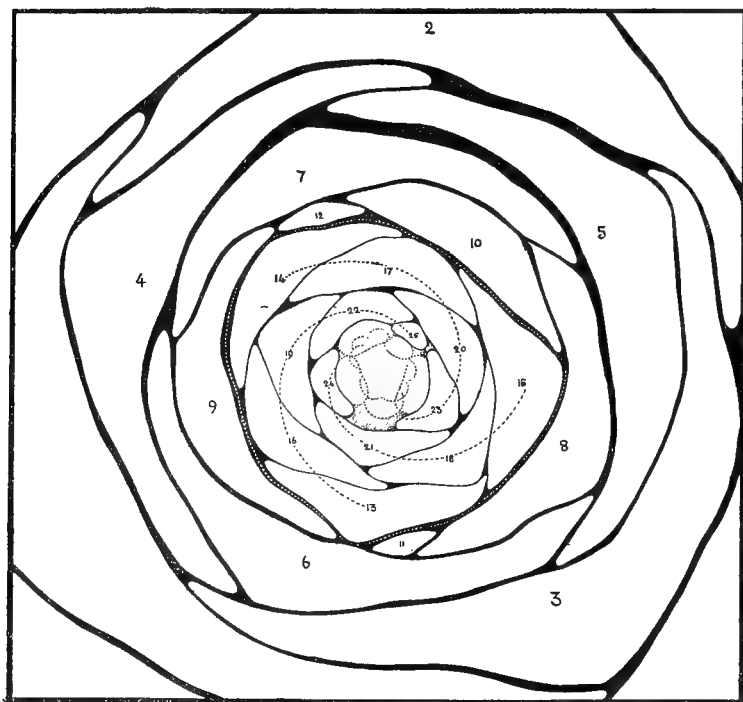
Fig. 52.—*Saxifraga umbrosa*, L. Section of perennating foliage-shoot (January):
$(2+3)$ system of previous year enclosing $(3+5)$ system of the new season's growth: the latter separated by a dotted line.

or first-year seedlings of *Nymphaea*, do not possess the $(5+8)$ system of the adult (*cf.* fig. 94).

The transition may take place at the commencement of a new season's growth as in *Saxifraga umbrosa*, or new curves may be added from time to time, as in the inflorescence of *Dipsacus*, to

* De Bary, *Comparative Anatomy*, p. 285.

keep up with the expansion of the axis. The preceding examples
of *Cyperus* and *Saxifraga* seem to show that as in the general case
of normal expanding phyllotaxis, the stations of stable equilibrium,
which are constituted by ratios in the Fibonacci series, are at-
tained as quickly as possible at any given transition.

FALLING PHYLLOTAXIS.

It now remains to consider to what extent the converse of these
generalisations will hold for reduction of the phyllotaxis systems.
That the same general principles obtain is shown by the inflor-
escence of *Dipsacus*, in which curves are dropped out with facility
equal to their interpolation, and here as in the stems of Cacti no
definite law holds, but one is put in or taken out as required to
adjust the bulk-ratio.

Comparison of the capitula of Compositae which exhibit the
perfection of expanding construction, shows that equal accuracy
does not obtain in the reducing stages, and that these are rather
of the type already included under the term " *discontinuous.*" So
far as can be determined, the reduction takes place more or less
irregularly, but on the whole the ratios of the Fibonacci series
continue to mark stations of equilibrium, and these when reached
may remain constant for a considerable period, though the arrange-
ment is not marked equally well in all cases. The alteration in
the bulk-ratio is not sufficient to present the optimum transition
which would maintain the set of the contact-parastichies unchanged;
but as this rises, reversal of the parastichies takes place, and a
consequent distortion of the system is therefore noticed at a greater
or less distance from the periphery of the system.

The reason for this is obvious : the log. spiral construction
which goes on for an infinite extent, however suitable for the
production of vegetative leaves, will not answer the purpose of the
capitulum, all the florets of which are required to produce seed
within a relatively short period.

In the *Helianthus* capitulum it is true that a uniform succession
of flowers in successively younger and smaller stages is maintained

to a considerable degree, but it cannot go on for ever. The system has a limit, and the system of progressive growth comes into conflict with the demand for the production of a mass of flowers approximately simultaneously.

To limit the series, the system must therefore be broken at certain intervals, and a lower series of curves, implying that the bulk-ratio has been raised, will be the sign of such modification.

Cynara Scolymus may be taken as a type (fig. 53*a*, *b*). The large capitulum commences formation of disk-florets with the ratio $(55+89)$, and this is continued as shown by the shorter curves for 8–10 members along these paths—that is to say, for an aggregate of about $9 \times 89 = 800$ florets. Since the meshes of the log. spiral network have all this time been getting smaller, though a theoretical construction diagram shows that the difference is almost imperceptible, a point is now reached at which adjustments in the lateral primordia can no longer be strained, and an alteration of the system correlated with a marked modification of the bulk-ratio is required. While the 55 long curves are thus carried on, the 89 short ones break off and present an approximate reduction to 34 still longer spirals—that is to say, the system is now $(34+55)$ and the set of the parastichies reversed. The transition is, however, not clearly marked, and it cannot be traced with sufficient accuracy to show whether it is rapid or irregular, owing to the fact that the actual leaves are absent. The point to note is that a Fibonacci ratio is soon regained. The " 34 " curves are carried almost to the centre of the disk, but at about six florets along the " 55 " curves these in turn break away, suggesting a reduction to 21, and implying therefore a second reversal to $(21+34)$. The central part of the disk becomes still more obscure.

The phenomena of falling phyllotaxis in *Cynara* somewhat resembles the rising phyllotaxis of the same capitulum, but with diminished accuracy. Expansion followed normal lines, but reduction gives discontinuous systems.

In the same way *Helianthus* presents reduction reversals, but they are less marked. For example, the head $(34+55)$, taken as a type (fig. 15), shows the short curves remaining unbroken for 11–12 members. The number of florets in which small adjustments were

PLATE XIII.
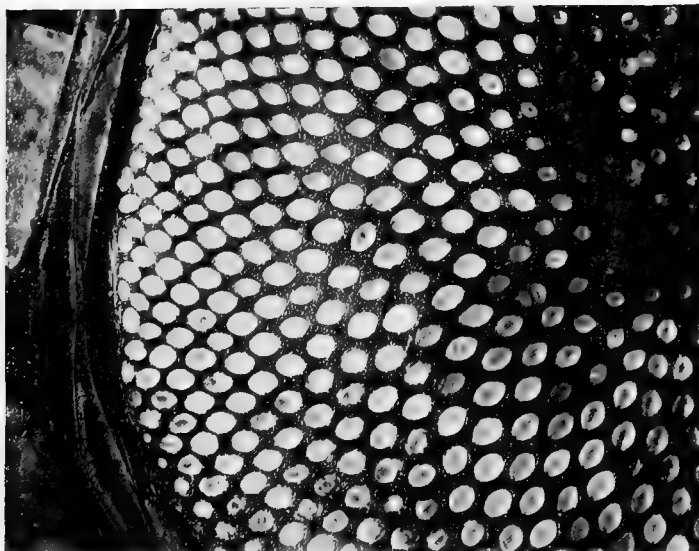
FIG. 53b.—*Cynara Scolymus.* Portion of the same capitulum magnified slightly, showing falling systems toward the centre.
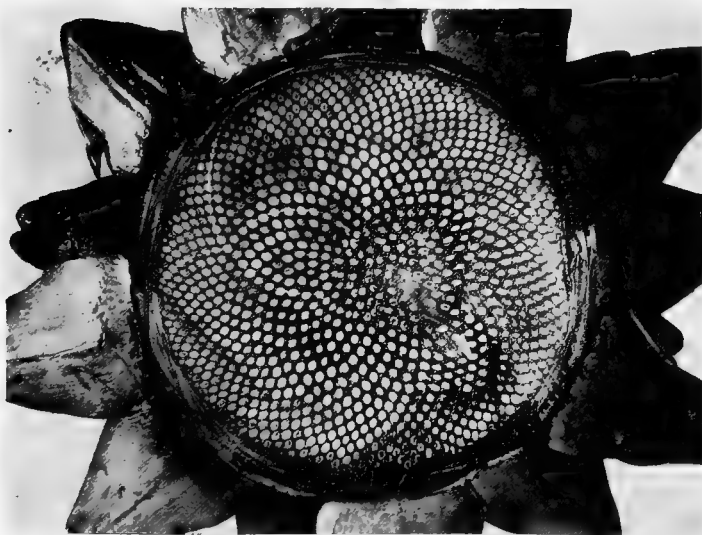
FIG. 53a.—*Cynara Scolymus*, L. Capitulum (55 + 89) shaved down to the ovaries of the disk-florets.

PLATE XIV.
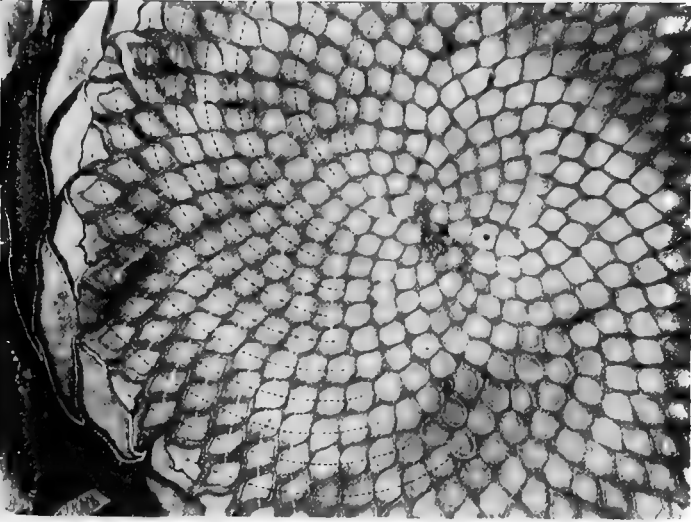
FIG. 54b.—*Helianthus annuus.* Portion of the same capitulum magnified slightly : the paths of the falling systems are dotted.
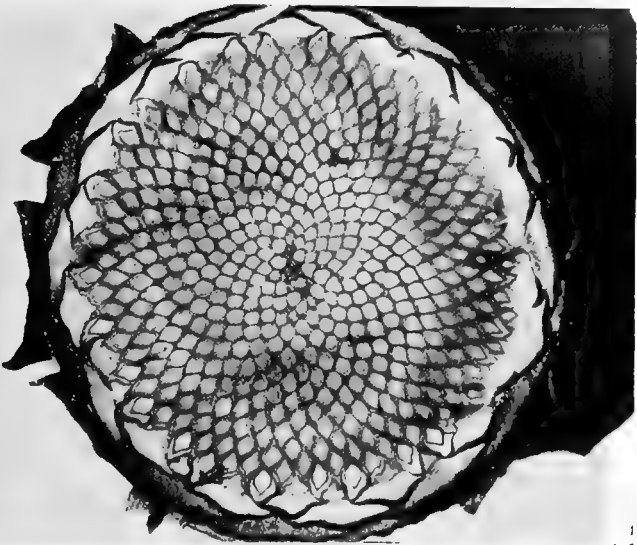
FIG. 54a.— *Helianthus annuus.* Anomalous capitulum, involucre (11 + 18) rising to disk-florets (29 + 47).

made before the system was altered and distortion ensued was thus 6–700. The large capitulum (89 + 144) (fig. 13), similarly shows unbroken short curves for 13–14 members, giving a total of nearly 1900 florets before the reduction set in. An anomalous head (29 + 47) (fig. 54), is only constant for about seven members along the shorter curves, or for a total of 320, the reduction taking place about half way in from the edge of the disk. In rare cases alteration may commence right on the edge and the parastichies then become too irregular to count. Although the general plan of reduction is clear, it does not appear to be sufficiently accurate to warrant the construction of theoretical diagrams. It is possible, however, that the actual change is still rapidly effected, and the mechanism of transition should again be denoted by a reduction in terms of the (2, 1, 2, 1, 2), etc., expression which marked the transit from one Fibonacci ratio to another.

Asymmetrical Constructions in Floral Diagrams.

Referring back now to the general scheme for the orientation of the cycles of the Schimper-Braun series (fig. 1), it becomes increasingly obvious that such constructions and their interpretations have no necessary connection with spiral systems, but are merely the expression of the relationship of successive terms of the Fibonacci series; and as already noted, Schimper and Braun added nothing to the Spiral Theory of Bonnet, but intercalated the Fibonacci ratios, which thus constitute an entirely independent generalisation. The fact that the tabulated orientations do agree with phenomena observed in the plant is really the expression of the rise of the Fibonacci ratios in the sequence 2, 1, 2, 1, 2, etc., as presenting the most symmetrical approximation to equal division of the new paths of growth.

It is further apparent that it is impossible to construct any accurate presentation of a spiral system in terms of circles; and as soon as circles are adopted, a source of error is introduced which leads one on unconsciously to further fallacies. It is impossible to interpret an asymmetrical system other than by spiral con-

struction, and the character of the spiral must therefore be known; yet the circular plan has been generally adopted in the construction of floral-diagrams. Take, for example, the "$\frac{2}{5}$" spiral, or *quincuncial* type, which characterises the calyx or perianth of the great majority of Dicotyledonous types: in the floral literature of the period which marks the evolution of the floral-diagram at the hands of the Wydler-Eichler school, from a mere transverse section of the flower-bud, one constantly comes across the tendency of older observers to deduce an abstract ideal type of construction which represented the general average of a mass of observations. Thus the remarkable prevalence of whorled arrangements in the floral members of the majority of floral types, which also holds to such an enormous extent in the ontogeny of the essential organs even when the calyx remains spiral, led to the assumption of a series of concentric circles as the basis of the floral-diagram; since again such circles were easy to draw, and spiral construction was not particularly obvious except in the case of a few of the Ranunculaceae and allied families, for which the application of theoretical diagrams was recognised as being extremely difficult. The introduction of the doctrines of evolution led to the result that these ideal generalised types were frequently interpreted as actual primitive forms, without any further phylogenetic evidence being required; circles were thus retained as being sufficiently accurate, and the "$\frac{2}{5}$" spiral thus became conventionally represented in terms of two circles, two members being placed on the outer and three in the inner, constituting the *Dicyclic calyx*.*

* Such a theory as that of the *Dicyclic calyx* affords a good example of the manner in which an abstract morphological generalisation, obtained from an average of a large number of observations, becomes mistaken for a phylogenetic one and ends by obscuring the very phenomena it was intended to elucidate. It is clear that the number of members selected by the plant to serve as a protective investment, or an attractive cycle, depends primarily on the relative tangential extension of these members: that $4 = (2+2)$ are most frequently selected in a dimerous flower, or $6 = (3+3)$ in the case of trimery, merely indicates that the members are relatively narrow, and subtend, when adult, an angle which is less than 180° or 120° as the case may be. Where the width is relatively considerable (*cf.* 2 sepals, *Papaver*, 3 sepals, *Tradescantia*), a single cycle suffices and is therefore employed; and the necessity for a dicyclic calyx thus falls to the ground. This subject will be further considered under the

Few systematists probably ever troubled about the question as to whether the helix of Bonnet and Schimper became an Archimedean spiral in the ground-plan; they accepted the construction and expressed the "orthostichies" of the genetic spiral as radii of the circle, assuming therefore that they were also radii vectores of the spiral.*

So long as this is regarded as a simple method of constructing a spiral system, and the convention is granted, no particular harm is done, and for conventional floral-diagrams the same construction may be retained so long as it is clearly understood that such a diagram does not present the facts of the given floral-structure accurately, but only a *symmetrical version* of them. Thus in a floral-diagram of the Buttercup, it is possible to place 8 oblique rows of stamens on a certain number of circles, or emphasise 13 rows on a smaller number, but the true $(8+13)$ construction, giving 8 oblique rows one way and 13 the other, requires a spiral curve. On the other hand, if the circular plan be adopted and the convention forgotten, error creeps in and may become magnified in the course of further deductions. Thus, having placed three members of a "$\frac{2}{5}$" spiral on one circle, and two on another, the next false step was readily made in assuming that the spiral either actually consisted of two such whorls in the plant, or might be interpreted as

---

heading "Varying growth in lateral members"; it thus becomes referable to the laws which control the tangential extension of foliar members, and discussion must therefore be postponed until the angles normally subtended by free and packed primordia have been tabulated for the different systems. (*Cf Mathematical Notes.*)

* It is of interest here to compare the views of Schleiden (*Grundriss der Botanik*, Eng. trans., p. 264), who in his masterly analysis of the principles of phyllotaxis as they were discussed in his day, stood alone among German botanists in his support of the theories of the Bravais, in that they were logically based on mathematical laws, and deduced from the properties of a "mathematical spiral"; the fact that an almost indefinite number of mathematical spirals may be proposed appears to have been completely forgotten. The spiral in question was a helix wound on a cylinder, which has a parallel screw-thread, but also makes equal angles with vertical lines drawn on the cylinder; it may thus be continued up a cone as a curve, which would on a projection give either a spiral of Archimedes or a logarithmic spiral, according as the former or latter property was allowed to determine the curve.

homologous to two whorls of three and two respectively; and this spiral series $(2+3)$ thus represented an intermediate condition between a whorled $(2+2)$ and a whorled $(3+3)$.

These were, in fact, the views of Eichler,* and constituted his theory as to the origin of a pentamerous flower, the effect of which is noticeable throughout the whole of his classical systematic work.

That the $(2+3)$ spiral system is intermediate between the $(2+2)$ and the $(3+3)$ systems is obvious. The first is an asymmetrical construction, the two latter symmetrical systems; but it does not follow that the "intermediate condition" is therefore a secondary derivative, while the $(2+2)$ and $(3+3)$ are primary formations. Eichler's interpretation naturally implies this peculiar standpoint, and trimery and dimery are thus regarded as more primitive than pentamery, notwithstanding the enormous preponderance of five "orthostichies" in vegetative shoots, a fact first noticed by Bonnet. However, this view being granted, it follows that Monocotyledons and trimerous and dimerous apetalous Dicotyledons must be the

---

* Reference to Eichler's Introduction (Blüthendiagramme I., II.) shows that these views apparently arose from a misinterpretation of the facts represented by the three types of flower in *Berberis vulgaris.* Thus a transverse section of the winter-bud (September) of a shoot which will flower in the next season shows foliage leaves in the contact relations of a $(2+3)$ system while the inflorescence bracts are apparently $(3+5)$. A longitudinal section of a later stage (November) shows the flowers developing, and brings out the remarkable fact that the terminal flower is the only one which has free space to grow. That this terminal flower should under these circumstances continue the system of the axis it terminates, and therefore present floral-members in five slightly spiral "vertical rows," as in *Delphinium Ajacis* (androecium), is perfectly natural, and this normally occurs. On the other hand, the lateral flowers, whether owing to specific tendencies, or the stimulus of close packing, tend to vary, and so give the natural symmetrical variants $(2+2)$ and $(3+3)$ of the $(2+3)$ system. One would not be surprised to find the normal type in a lateral flower, or the $(3+3)$ in a terminal, if these variations are determined solely by the plant, and such again are the facts observed. The fact that the plant selects a certain number of members to act as perianth segments and sporophylls in the different cases, is wholly secondary to the mechanical construction which originally produced them ; the rule the plant adopts is to take as many as will completely fill a circle round the axis for each kind of member it requires, this being 4, 5, 6 for the three types respectively, as shown by the proper geometrical construction in terms of the numbers of curves.

primitive floral types; the fact that the majority of these again are whorled, while in a great many the vegetative shoots remain in the spiral condition, apparently presenting no difficulty. Simultaneously with the introduction of these ideas, Gymnosperms were becoming finally separated from Dicotyledons, and the further fallacy was interpolated, that since Angiosperms must have passed through a Gymnospermic condition, that condition must necessarily be the same as that observed in recent Gymnosperms which happen to be all diclinous anemophilous tree-types; and thus in spite of the teaching of the heterosporous Vascular Cryptogams, dicliny as a primitive condition became added to dimery. The general lines of the Decandollean classification, followed in this country by Bentham and Hooker, were consequently more or less inverted; and it is so far possible that the systematic work of the Eichler-Engler school rests on a very fallacious basis. It is to be hoped that at no very distant date the pendulum will again swing back to the Decandollean standpoint, since it is increasingly evident that no hypothesis as to the phylogeny of Angiosperm families can ever be acceptable to morphologists which is not based on the standpoint that floral axes and members primarily obey the same mechanical laws of construction as obtain in asymmetrical vegetative shoots, and therefore originally followed the same simple Fibonacci ratio systems: that all primitive floral types were therefore necessarily asymmetrical in construction, and produced a considerable number of members in an *indefinite* system; the often abused term "indefinite" being used in the sense pointed out by Schleiden as its only logical meaning, *i.e.*, a construction in which lateral members are set apart for their special functions in an indefinite number along the same genetic spiral.

The fact that the present position of Systematic Botany may be wholly erroneous, and that its errors may be traced back, in part at least, to the neglect of the correct presentation of spiral construction, may prove to be historically interesting.

Without going into further detail at present as to the construction of floral-shoots, it may be pointed out that evidence will be subsequently adduced to show that the vast majority of floral-structures may be reduced to derivatives of two common asym-

metrical constructions only,—the $(2+3)$ and the $(3+5)$, from both of which pentamerous forms may be obtained.

I. The rules for constant phyllotaxis may be observed; *e.g.*, in *Delphinium Ajacis*, $(3+5)$ throughout; *Calycanthus*, $(5+8)$ throughout.

II. Normal expansion types are general among the primitive forms; *e.g.*, Ranunculaceae and allied families exhibiting very commonly $(2+3)$ $(5+8)$, *Nigella*, *Magnolia*; $(3+5)$ $(8+13)$ *Helleborus*, *Aconitum Napellus*.

III. The symmetrical variations of the form,—

$(2+3)$ becomes $(2+2)$ or $(3+3)$,
$(3+5)$ becomes $(3+3)$ or $(5+5)$,

follow normal lines of production, by the equalisation of the parastichy curves; the full type thus commences by adding normally to the long curves, but remains stationary on the first attainment of symmetry, while true dimery and trimery are seen to be secondary, as dicliny also undoubtedly is as well.
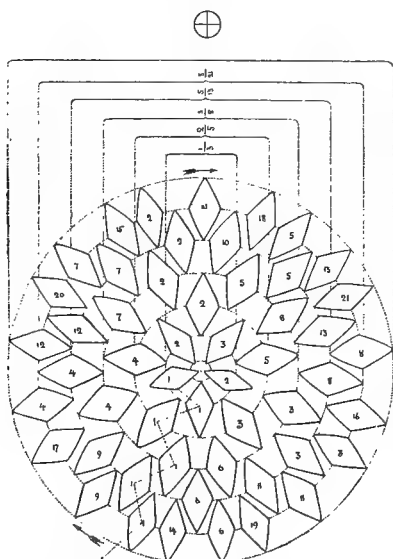
Fig. 1.—Symmetrical version of falling phyllotaxis in terms of circular construction instead of spiral.

IV. The case of falling phyllotaxis is rendered especially interesting, in that such a reduced series naturally closes the production of lateral members at the end of the floral axis and will be noticed usually in the members of the gynoecium (Ranunculaceae).

The general phenomena of such a falling phyllotaxis having been described as theoretically representing a fall of the Fibonacci ratios along their normal sequence 2, 1, 2, 1, 2, etc., the scheme

already presented in fig. 1, as including such a descending series of terms arranged on a circular plan, becomes a valuable convention for the satisfactory completion of the floral diagram of such a type, in that, when the circles are cleaned out, it cannot be distinguished by the eye from the appearances presented by the plant; while at the same time it retains in its construction the theoretical suggestion of what true reduction should have been if it had taken place equally all round the axis.

IV. The Symmetrical Concentrated Type.

THIS, the most highly perfected condition of phyllotaxis, is met with more especially in the mechanisms of flowers, and also in specialised assimilating shoots (*Hippuris, Labiatae, Oleaceae, Equisetineae, Dasycladeae, Characeae*) presenting the case of " alternating whorls." In the theory of Schimper and Braun it can only be derived from a' spiral system, by complicated processes of " Prosenthesis"; while, on the other hand, very curious hypotheses that spiral arrangement is secondary and derived ontogenetically from primitive whorled conditions have been put forward by Henslow and Airy.*

It is sufficiently clear, however, that these latter views ignore the normal facts of spiral development as expressed by Hofmeister; and previous considerations of the normal asymmetrical concentrated type indicate that the " concentration " of the system is one of the surest marks of its origin from the corresponding asymmetrical case, by the assumption of true circular symmetry as a special case of log. spiral construction. The system is thus simply defined by the number of members in the alternating series, and accurately planned in a diagram by symmetrical pairs of mutually orthogonally-intersecting log. spiral parastichies; *i.e.*, when the number of members is very large, the construction is checked by counting an *equal number* of contact-parastichies in either direction (fig. 55). It may be derived from the preceding type either phylogenetically or ontogenetically, by the growing zone becoming at any stage

* *Trans. Linn. Soc.*, ser. ii. vol. i. 1875. *Proc. Roy. Soc.*, vol. **xxii.**, 1874, 297–307.

definitely symmetrical, and thus producing a series of members simultaneously instead of one by one.

The specialisation of the construction is thus simply indicated : the cumbrous method of building a radial system by the addition of individual members, which initiates the mechanism of the pre-
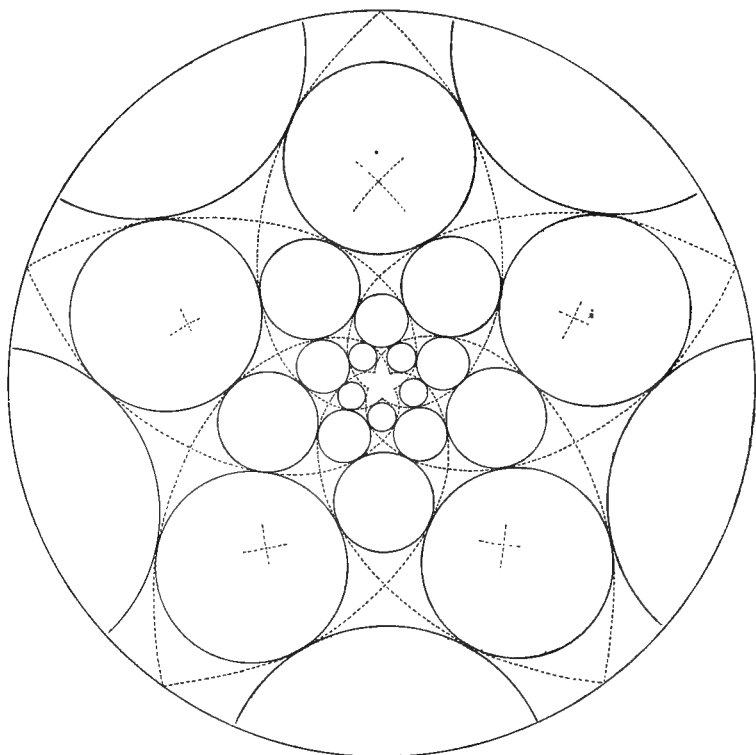
Fig. 55.—Symmetrical construction (5 + 5), representing the condition of true pentamery as observed in the flowers of many Dicotyledons.

ceding type, is swept away *ab initio*, and with it vanishes all the preceding geometrical considerations of spiral-vortices, ideal angles, and restricted attempts at symmetry.

How small the actual change may be in a given apex, is indicated by the close approximation of the genetic spiral to a circle,

K

and the approximately equal bulk of the members of one cycle in the higher ratios of spiral phyllotaxis; as also, in actual ontogeny, by the imperceptible differences of time between their serial formation when growth is at all rapid.

The determination of the number of members composing a whorl remains wholly a property of the protoplasm, though the marked constancy in the retention of the number 5 in the flowers of Dicotyledons, corresponding to an advance on the asymmetrical system $(3+5)$, indicates the influence of phylogeny on subsequent specialisation; on the other hand, the readiness with which whorled pentamerous flowers vary to 6- and 4-merous, and trimerous to 4- and 2-merous, shows an increased plasticity in the system, and that *with the assumption of a true symmetrical construction, the causes which led to the adoption of the series of Fibonacci must also have been eliminated.*

The same elimination of this series of numbers is observable in the progressive rise of members in a whorl in correlation with an expanding axis bearing more constant members (*Neomeris*), and again in the progressive reduction of members along successive degrees of ramification (*Equisetum*).

Special interest attaches to the lower members of the series, *i.e.*, those in which one or two pairs of symmetrical curves plot out the construction. The former gives the symmetrical formation of alternating members in two rows at angles of 180°, generally known as the *distichous* condition.

The latter, produced by two pairs of curves, on axes at 180°, is that usually known as the *Decussate* system, giving four vertical orthostichies. This appears to be very constantly correlated with xerophytic specialisations in the assimilating system, and is often quite independent of any dimery in the floral members (*Clematis, Calycanthus, Labiatae*). It is remarkable in that it presents the first *doubled system*; and while it could not be produced from two concurrent genetic spirals, it is possible that, given such a doubled curve-system, secondary reversion to the asymmetrical condition might be initiated from either pair, and a doubled spiral system be the result.

That the decussate system may be also produced as a variation

of whorled trimery is further shown by the case of reduced Monocotyledonous flowers ; *e.g.*, individual flowers of *Iris, Lilium*.

The case of three symmetrical pairs of curves at angles of 120° which gives the typical trimerous Monocotyledonous flower, here represents the full symmetrical case of the system $(2+3)$, as is shown by the partial retention of the spiral in ontogeny (*Lilium candidum*, etc.); but it may also occur as a variation of a decussate type, as in the assimilating shoots of *Fuchsia gracilis, Fraxinus, Impatiens*, and again as an extreme reduction of a pentamerous flower passing through the tetramerous phase and thus independent of the ratio series (*Oenothera biennis*).

Similarly the case of whorls of four members may have a threefold origin, to be separated carefully in the consideration of floral phylogeny : firstly, as an extreme variation of the decussate system (foliage shoots of *Fuchsia gracilis*); secondly, an advance variation of trimery, flowers of *Crocus, Iris, Leucojum, Lilium* (more constant in *Paris*); and lastly, a reduction variation from pentamery, the most general case of tetramery, as found in the flowers of *Oenothera, Alchemilla, Cruciferae* ; and less frequently, *Ruta, Jasminum, Euonymus, Ampelopsis, Viburnum*, etc., etc. In the same way true hexamery may be produced as a variant of pentamery, as in flowers of *Ruta, Jasminum, Ampelopsis, Viburnum, Heracleum*, etc., supplying increasing evidence that with perfect symmetry in construction the value of the series of Fibonacci is completely lost, although the phylogenetic relics persist to a very considerable degree; due, no doubt, in many cases to the fact that symmetry is only attained in the specialised floral mechanism, while the parent shoot still retains its unmodified asymmetrical and mechanical construction, so long as there is no direct advantage to be gained by substituting either radial or dorsiventral symmetry.

As in the case of asymmetrical constructions, it is easy by making geometrical drawings to obtain an idea of the bulk-ratio for any given symmetrical system with a degree of accuracy quite sufficient for any practical purposes, the ovoid curves inscribed in the log. spiral meshes being taken as circles.

The following table expresses these results:—

Whorls of	Bulk-ratio.	Angle subtended by circle.	Angle subtended by rhomb ("square").
2	$\left(\begin{array}{c}1\cdot2 : 1\\ 1\cdot5 : 1\end{array}\right)$	$\left(\begin{array}{c}115^{\circ}\\ 80^{\circ}\end{array}\right)$	180°
3			120°
4	2 : 1	60°	90°
5	2·4 : 1	48°	72°
6	2·8 : 1	41°	60°
7	3·3 : 1	35°	51°⅗
8	3·7 : 1	31°	45°
9	4·1 : 1	28°	40°
10	4·6 : 1	25°	36°

Inspection of the bulk-ratio column, which may be assumed to be fairly accurate when the angle subtended is 60 degrees or less, is sufficient to show that the rise from pentamery to hexamery, for example, would represent a comparatively small variation as expressed in the formation of a larger and better nourished axis which tended to produce members of a constant type.

The diagrams also illustrate the fact that whorled tetramery has almost identically the same bulk-ratio as the (3 + 5) asymmetrical system from which a spiral pentamerous flower is phylogenetically derived; while whorled hexamery almost equally approximates the bulk-ratio 3 : 1 of the asymmetrical (5 + 8) system.

It is easy to adduce facts which fall into line with such generalisations, although they do not necessarily add any proof of the theory; for example, the latter case is of interest in connection with the readiness with which terminal flowers of *Campanula media* vary to symmetrical hexamery when the vegetative main shoot presents the (5 + 8) asymmetry.

As an example of the perfect irregularity of the symmetrical expanding construction, and its absolute independence of the Fibonacci series, the vegetative shoots of *Equisetum Telmateia* afford conspicuous illustration.

For example: a weak foliage shoot of 32 nodes, the continuation of a rhizome bearing leaves in whorls of 10–11, showed a rapid

rise at first, culminating in a maximum at the 13th node, with a gradual fall towards the slender apex; the whole shoot being of a spindle shape in the bud and the leaf members approximately constant in volume.

The leaves at successive nodes were as follows:—

11, 13, 14, 14, 17, 20, 20, 22, 24, 27, 28, 29, 30 ; 29, 30, 26, 26 ; 26, 23, 23, 21, 19, 16, 14, 12, 9, 8, 6, 6, 4, 3.

The number thus ultimately falls to 3, which possibly represents the ancestral number derived from the three segments of the apical cell, as in the similarly constructed apex of the leafy gametophyte axis of many mosses; although it is difficult to prove, even in *Equisetum*, that since the protuberances which indicate the primordia appear to involve these segments, they are necessarily dependent on the histological segmentation.

Another strong shoot (May 1901) including 40 internodes gave similar results : springing from a rhizome of uniform construction with 13 members in a whorl, the shoot reached the level of the soil in 5 internodes, 13, 13, 16, 18, 22 respectively ; the maximum was reached in 12 internodes, the additional ones being 24, 27, 28, 30, 33, 34, 36 respectively. As in the previous example, this maximum condition was succeeded by a region in which variation took place, the numbers for the next 5 nodes being 34, 36, 32, 34, 35. A steady descent then set in and was continued for the remaining 23 nodes :—36, 34, 32, 30, 30, 30, 29, 27, 26, 24, 24, 22, 20, 17, 14, 12, 9, 6, 5, 5, 4, 4, 4.

Equisetum Telmateia thus affords an excellent example of the possible independence of each nodal-formation of a symmetrical system ; the bulk-ratio is independently arranged for each cycle of members, and although it may remain constant when only a few large primordia are inserted, the curious oscillation period between the rising and falling series shows that in the case of relatively very small primordia the mechanism is imperfect and only approximates the number at each node.   Similar phenomena occur in the *Dasycladaceae (Neomeris)* ; in *Equisetum* they become the more striking, in that very regular constructions are often postulated for the stelar system, which is only secondary to that of the leaves, and thus less accurate than is generally supposed.

Applying these generalisations to the simpler members of the series, it would appear probable, then, that given a primordium subtending a considerable angle, the chances of variation between successive whorls of members would be correspondingly decreased. The difference between three members in a whorl and four, for
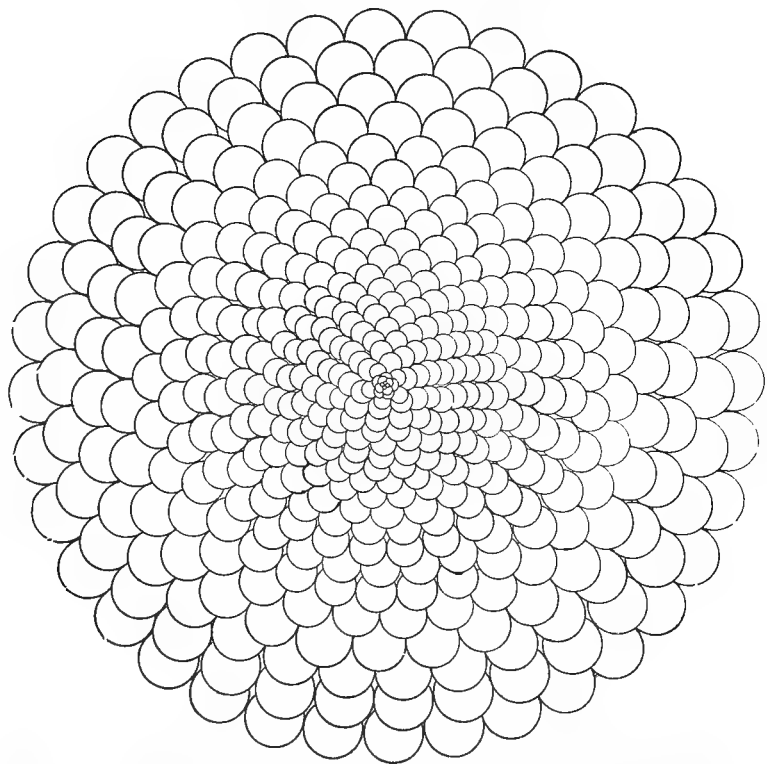
Fig. 56.—Descending symmetrical phyllotaxis: geometrical representation of the apex of a shoot of *Equisetum Telmateia*, showing irregular parastichies.

example, being considerable, it would be expected that individual or specific variations to tetramery, or from pentamery to hexamery, should, when they occur, affect all the whorls of the shoot, and this in fact is the general case. The occurrence of such a condition as that observed in a starved plant of *Cucurbita Pepo*, which is normally

very constantly pentamerous, in which 4 sepals were followed by 3 petals and the anther lobes of 2 stamens, would form so marked an exception that it would be readily recognised as a deformity.   It will further be noted that, expressed in terms of the parastichy curves, a symmetrical whorl of 4 members will be contained by (4 + 4) curves, and a whorl of 5, (5 + 5), etc.   It thus follows that any change in a symmetrical system, in which symmetry is retained from node to node, implies the addition or loss of at least two curves simultaneously, one in either direction, since the addition or loss of an uneven number would at once throw the construction into an asymmetrical form.

That the increase or reduction of the members of a whorled system may often be due to variations in nutrition, so that the bulk-ratio may be involved in a manner similar to that described for asymmetrical types, is clearly suggested by the enormous range of variations observable in some flowers, especially *Papaver somniferum*; under varying conditions of cultivation the number of carpels which may reach 15 in a strong plant readily falls to a minimum 4 in progressively starved plants, while the aggregate number of stamens which present an irregularly symmetrical system may be simultaneously reduced from over 500 to 8.

Better examples are met with in the progressive reduction along successive axes of the same plant, homologous again with the reduction along the members of the Fibonacci ratios in successive ramifications previously noted (*Helianthus*, etc.), but differing again in the complete absence of these values, and thus affording a much more gradual decline: *e.g.*, *Ruta* commonly produces terminal 6–5-merous flowers, while 4-merous are practically constant in the ultimate scorpioid cymes.   Most striking is the case of *Sempervivum*: three plants of *S. italicum*, growing in the same pot, gave the following numbers for the sepals and petals of successive floral axes (the construction is not absolutely constant throughout individual flowers) :—

	T.	T$_{\mathrm{I}}$	T$_{\mathrm{II.}}$	T$_{\mathrm{III.}}$	T$_{\mathrm{IV.}}$	T$_{\mathrm{V.}}$	T$_{\mathrm{VI.}}$
		⎧ 12	13	12	11	11	10
I. . .	14	⎨ 13	12	12	12	11	
		⎩ 12	13	11	11	11	

	T.	T^I.	T^II.	T^III.	T^IV.	T^V.	T^VI.
II. . .	15	14	12	12	12	11	11
		12	12	12	11	11	10
		13	11	10	10		12	
			12	12	12	12	11
III. . .	14	12	12	11	11		
		12	13	12	12		
		12	12	11			
		12	13	11	13		

the reduction being thus fairly progressive from 15 to 10 along the ultimate ramifications.

The case of *Equisetum* further illustrates the mechanism of addition and loss of members. No rules are here applicable; the number added may be quite irregular, and in the case of falling symmetrical phyllotaxis, the amount of adjustment required in the mechanism must be very considerable. So marked is the rising and falling sequence in the vegetative shoot of *E. Telmateia*, and so relatively short is the region over which a constant phyllotaxis would be possible, that it may be said that this plant never possesses anything better than an irregularly symmetrical construction; the obvious part of the whorled appearance being produced by the adjustment of the secondary zones of growth which constitute the internodes. The apical portion of such a plant may be taken as a type of " irregular symmetry," which is again a distinct phenomenon from normal asymmetry, but, as will be seen, incapable of distinction as a *primary* phyllotaxis construction from irregular asymmetry.

Taking the latter example of *E. Telmateia*,* and translating it into

---

* It will be noticed that this affords what may be termed an architectural conception of the *Equisetum* shoot, based on the view that all the leaf members are of equal value, and that *Equisetum* is only a modern highly xerophytic edition of a plant which once presented normal vegetative leaves ; on the other hand, it does not accord with the accepted versions of the construction of the apex of such a shoot, usually found in text-books, the older researches on this plant having been conducted from the standpoint of the dominant influence of the apical cell (Hofmeister, Reess, Cramer). Once this cell is deposed from authority, it will be seen that it is extremely difficult to prove whether the *annular ridge* really belongs to a cycle of three segments which have been "a little displaced" (Reess), or may not equally well be regarded as the result of an independent symmetrical annular impulse which must nearly approximate these superficial cells. The same annular ridge again represents such an early gamo-

a diagram in the transverse plane, in the form of a floral-diagram, by placing the observed number of apparently perfectly similar members on a series of concentric circles to represent the whorls, a scheme will be plotted out which is therefore identically that of the telescoped axis (fig. 56).   In such an irregular system the parastichies present a hopeless medley, straight in places, curved in others, but still roughly equal in number when counted in either direction, at a given level, so far as they can be counted.   When the construction circles are rubbed out, no interpretation of such a condensed system is possible to the eye ; in *Equisetum*, the symmetrical condition is rendered obvious by precocious gamophylly and secondary elongation of the system ; but in the absence of such a second zone of growth, it is evident that it could only be included under the loose term " indefinite," and that no such system can be verified nor can the construction be described.   When such constructions occur in flowers, as very noticeably for example in *Clematis*, it is possible to regard it as a degenerate symmetrical one, when as in this case the whole of the other phyllotaxis relations of the plant are symmetrical ; but it is clear that all reduction systems must closely resemble one another in their capacity for becoming undeterminable.

In the presence of a primary phyllotaxis system, therefore, whether in the case of asymmetry or symmetry, it is only possible to give an

phylly of the lateral members that it is evident that leaf-production is no longer normal, while the interpretation of " primary and secondary teeth" (Reess) is also doubtful.   Thus Hofmeister, when he first investigated the apex, called the whole sheath one leaf which produced more teeth as it became older (which is certainly one way of interpreting the termination of the shoot as expressed in fig. 56), and that 4 was the primary number (*Higher Cryptogamia*, 1862, p. 270). Reess futher admitted the possibility of the formation of a number of primary teeth (7–8), of which 3 was not a factor, so that the sextant segments must have been unequally affected.   It is remarkable that these views should have been accepted without any drawings or accurate evidence in favour of them ; the fact that the annular ridge is formed quite independently of the apical segmentation being sufficiently clear to the unprejudiced eye.   (*Cf.* Cramer's drawings, *Pflanzenphys. Unters.*, Nägeli und Cramer, iii. plate xxxiii. figs. 19, 20 ; xxxiv. 1–3 ; also in text-books.)   The same fact has been pointed out by Schwendener (*Botanishche Mittheilungen*, vol. i. p. 153), who examined the critical case of *E. scirpoides*, with the cycle of three members.   There is thus no doubt that the symmetrical formation of the impulses which produce the lateral members is wholly independent of the asymmetrical segmentation into cell-units.

account of the phenomena when the construction remains constant for a period sufficient to give by recapitulation the appearance of definite contact-parastichies ; an unequal number of intersecting curves means asymmetrical construction, an equal number implies true symmetry.

The slightest deviation from absolute symmetry produces an apparent spiral effect, just as the failure of a circle to come round on itself in the smallest degree would produce a spiral curve, and the subjective effect, as judged by the eye and interpreted in terminology, is quite disproportionate to the cause.

Thus the parastichies of wall-papers and tiles on a roof, quoted by Sachs, are as clearly the expression of a symmetrical construction as the vertical and horizontal lines of the pattern. Equally good examples are often seen in the arrangement of imbricating ovules in an ovary (*Asclepias*) or scale-emergences on fruits, etc. (*Raphia*, Acorn-cup); so long as the construction is regular, the secondary " parastichies" present an equal number in either direction; but the slightest deviation from strict regularity at once renders these curves unequal or irregular, and a spiral system is the result. Thus in the Sago-Palm fruit (*Raphia*, fig. 72), the emergences are relatively very large, and when regularly formed they fall into series giving symmetrical curves $(6+6)$, $(7+7)$; but any trifling irregularity in formation spoils these rows, and thus $(6+7)$ is equally common: the secondary spiral appearance thus produced does not imply that the scales constitute a phyllotaxis system, or that the members are leaves, although regarded merely as adult structures the resemblance is very striking; the suggestion that this similitude in lateral appendages of different value morphologically may be the outcome of a common law of growth is very obvious.

The phyllotaxis phenomena of whorls and spirals observed on the plant are thus merely the outward expression of the distinction between symmetrical and asymmetrical construction. In the primary system, seen in Zone I., when the original lateral contacts are maintained, the most obvious sign of the mode of growth is the equality or inequality of the diagonal construction lines (parastichies), these being more readily checked by the eye than the complementary lines of construction, which may be circles or

spirals hard to differentiate. The mathematical fact that the number of members represented by the integer which is a common factor of this parastichy ratio are of identical value, becomes expressed in the number of members left at a node when the internodes are subjected to secondary elongation. If the parastichy ratios are equal, the system pulls out as rings of members of the same number, and a similar number of subjective spirals may be drawn diagonally from node to node; if they are unequal, but divisible by a common factor, for example 3, then 3 members are left at each node and 3 spirals may be so drawn in one direction; but if divisible by unity only, a single member is left isolated at a node, and the one subjective spiral which may be drawn through the whole system becomes dignified by the name of "genetic-spiral," in that it attains an enhanced ontogenetic value according as the rate of production of the system in *time* becomes decreased.*

* Since the postulated change in the mechanism of symmetry involves the addition or loss of construction curves at least two at a time, it becomes of interest to see to what extent deviations from such a symmetrical change may be found. Thus the addition or loss of one curve only would produce immediate asymmetry which would be expressed by a transition from whorls to spirals. Such a spiral series would again be of the maximum-concentrated type, since the contact-parastichies would only differ by 1, and would possess as a complementary system the least-concentrated type, in which one spiral passes through all the members as a contact-line, and winds around the stem (*cf.* fig. 36). The extent to which such a genetic spiral becomes obvious to the eye may differ according to circumstances. *Cf. Lycopodium Selago* (5 + 6) and Cactaceae (6 + 7), in which the construction is not seen on the cylindrical axis, but is readily observed in section of the apex, or on the apex as in Cacti. On the other hand, it has already been pointed out that the symmetrical development of the foliar members in *Equisetum* is marked by congenital gamophylly; a transition to the asymmetrical condition would therefore be expected to show similar gamophylly along the course of the ontogenetic path, and the lateral members thus form a spiral fan winding round the axis. Such variations have been frequently described as monstrosities (Milde, Reinsch), and spiral portions may thus be intercalated in a whorled system.

Cf. Reinsch, *Equisetum Telmateia*; *Flora*, 1853, Taf. ii. fig. 3, p. 69 (a spiral for 203 members intercalated between whorls of 30 and 28); *Flora*, 1860, p. 737, Taf. vii. fig. 9. A similar reversion to asymmetry is described for *Hippuris* and *Casuarina* (Reinsch); while it is of interest to compare the spiral ridge thus formed in *Equisetum* along the genetic-spiral of such systems with the ridges of Cacti which often follow the paths orthogonal to the genetic spiral (phyllody spirals, fig. 63).

V. Asymmetrical Least-Concentrated Type.

IN its simplest form, as expressed in terms of single cells, this is the condition which obtains in the derivatives of the three-sided apical cell of Ferns, Equiseta, and Muscineae, where the three series of segments form superposed series; a line joining their centres of construction becomes the ontogenetic log. spiral, while the three lines passing radially through the centres of construction of the superposed segments also form three log. spirals, so that no two members are mathematically superposed, within any limit of construction. The system is thus defined by the number of these "vertical" spiral rows.

In the case of the cell-segments of *Pteris* root-apex, these log. spirals were not obvious, owing to the fact that only a few members are shown in one transverse section, although, owing to their rectangular construction closely approximating 1 : 5, more members were seen than can be plotted out in a normal orthogonal curve system. The fact that the arrangement naturally follows from the presence of a three-sided cell, in which each segment produces a foliar outgrowth, while the presence of the three-sided apical cell may itself be a sign of a primitive method of concentrating the terminal ramifications of a filamentous Algal type, lends considerable weight to the view that this method may be phylogenetically one of the oldest constructions, so far as it occurs in Mosses.*

* Cases in which the relative size of the cell constituents of the plant-body is so great that the arrangement of the lateral members is apparently within the control of single cells, may be conveniently left for the present, and the discussion of phyllotaxis confined to those cases in which the space form of the organism is

In Filicineae and Equiseta, however, considerable departures have been made from the type so far as the origin of the lateral foliar members is concerned.   Thus, while in *Equisetum* circular symmetry is apparent almost immediately behind the apex, and the number of members in a whorl of leaves is by no means necessarily a number of which three is a factor, nor bears any relation to the series of Fibonacci ; on the other hand, in Ferns, a specialised concentrated system may be in full operation, and thus *Aspidium Filix-Mas*, with a three-sided apical cell, produces foliar members and a correlated stelar meshwork in the system $(5+8)$, $(3+5)$, or $(2+3)$ (fig. 35).*

independent of its histological composition.   The limitation, for the present, of the term "leaf" to such a massive protuberance avoids the difficulty of distinguishing between leaves, branches, or mere hairs in Algal forms.   Special interest attaches to the three-sided cell of the *Muscineae*, since this directly cuts off the segments which become lateral members, and in that in the majority of forms, the arrangement of leaves becomes discussed in terms of the Fibonacci series.   Thus *Fontinalis antipyretica*, with a tetrahedral cell like that of *Equisetum*, gives keeled leaves in three well-marked spires, which straighten out on elongated shoots, but on short thick ones compare with the spires of *Pandanus* (Goebel, Leitgeb.).   In other cases (*Polytrichum formosum* type) the apical cell divides by *oblique septa* in a constant manner, giving three series of oblique segments, the three spires being so much exaggerated that " orthostichies" may be expressed, in high ratios, of both Fibonacci and anomalous series (Hofmeister, Müller, Lorentz, Goebel).   Torsion is admittedly absent (Goebel), and the leaf-traces in the stem follow the same coiled three-spired series.   It thus becomes a question as to whether this oblique segmentation is really the cause or a consequence of the formation of new growth-centres in a definite manner within the substance of the apical cell, and that the whole mechanism of asymmetrical growth, which in more massive plants produces a Fibonacci system of cell-aggregates, is not here enchained by the necessities of cell-segmentation, so that the new lateral growth-centres are never sufficiently free to assume the homologue of a spherical form, correlated with a centric distribution of growth-energy ; and the exigences of histological division may thus effectually mask the true asymmetrical construction.   It may be noted that the oblique leaf segments ultimately produce very fairly symmetrical leaf-forms, and that the space-form of the adult shoot compares very favourably with that of ordinary leafy stems.   (*Cf.* Goebel in *Schenk's Handbuch*, vol. ii. p. 373 ; Müller, *Prings. Jahrb.*, vol. v. p. 247 ; Engler and Prantl, *Nat. Pflanz. Fam.*, Musci, p. 178).

    * De Bary, *Comparative Anatomy*, p. 285.

    Hofmeister attempted to derive the $\frac{5}{13}$ phyllotaxis of *Aspidium Filix-mas* from the segmentation of the three-sided apical cell, although the segment walls were clearly parallel to the sides.   Hofmeister's view that the genetic spiral was necessarily *homodromous* with the cell-spiral and each segment gave a leaf, is

It has been previously pointed out that the concentrated and non-concentrated *symmetrical* conditions are only the limiting cases of spiral constructions which vary in the degree of concentration, all being concentrated to a certain extent in relation to the case of superposed whorls ; the most concentrated asymmetrical system being that in which the number of intersecting parastichies most nearly approximates equality ; the least concentrated, that in which they differ most widely.

It is thus clear that the least concentrated types must have one of the members of the ratio unity, and the lowest members of the normal phyllotaxis series $(1+1)$, $(1+2)$ may be therefore isolated as representatives of such systems. In this construction other contact parastichies are necessarily wholly absent (*cf.* Scheme B, fig. 20) ; *the one long curve becomes the ontogenetic spiral, and the log. spiral shorter curves become vertical spiral rows which may be conveniently described as " spires."*

Thus the two-spired type occurs in *Gasteria* (figs. 57*b*, 58*a*), and the three-spired type in *Cyperus, Pandanus, Apicra spiralis* (fig. 59*a*, *b*). Such two-spired plants occur in species of *Gasteria* mingled, on the one hand, with specimens exhibiting normal ratio-series $(3+5)$ or $(2+3)$, *Gasteria ensifolia, G. candicans*; and, on the other hand, with the special case of symmetrical $(1+1)$ construction, *G. obtusifolia* (fig. 57*a*).

So closely are these connected that seedlings vary in the same batch (fig. 58*b*). As the succulent dorsiventral leaves spread out, the two spires become very pronounced ; but any assumption of torsion in one plant more than another, or, in fact, in any such

obviously put out of court by the fact that the phyllotaxis spiral is often *antidromous*, and normal Fibonacci phyllotaxis phenomena may be found associated with a two-sided apical cell. (*Cf.* Schwendener, *Botanische Mittheilungen*, vol. i. p. 156.)

Nor was there ever any evidence in support of the older view beyond the standpoint of the dominance of so special a mode of cell-construction. On the other hand, comparison of *Equisetum* and *Aspidium* show that whatever the " growth-centre " may be, or whatever its nature, it is not localised in the nucleus of the apical cell, but must be either a finite mass larger in these cases than a single cell, or else represents a general function of the whole protoplasmic substance of the apex comparable with the somewhat allied conception of Polarity.

succulent forms, in order to space out these leaves to better advantage with regard to light, is clearly out of the question, when the xerophytic structure indicates that such exposure is not desired and is as purposely avoided by assumption of the symmetry as in the parallel decussate type.

> Since $(1+1)$ gives a normal symmetrical construction with one member only at a node, it is difficult to bring these two-spired types into line with the normal asymmetrical series. The deflection of the members is so slight that it appears possible to regard the case as one in which the $(1+1)$ generating curves become slightly unequal, and thus produce asymmetry of the form $1 : (1+a)$, where a is very small. From this point of view the two-spired *Gasteria* becomes of greatest interest, in that it appears to present an example of secondary symmetry which is with difficulty maintained from node to node, *i.e.*, the curve does not keep true.

The three-spired type, familiar in the leafy shoots of *Pandanus* and *Cyperus*, is apparently similarly derived from a $(1+2)$ system. A transverse section of the foliage-bud of *Cyperus alternifolius* shows the three spires very clearly (fig. 51), while the course of the genetic-spiral is as clearly marked as in the case of the segments of the apical cell of the Fern-root (fig. 51, left-hand spiral through 1–9). The spires become again obvious when the axillary reproductive axes are developed in ascending series in November–December (fig. 59*b*).

> The leaves of Cyperus are highly specialised from a biological standpoint. The first formed members on a shoot are wholly sheathing, so that their phyllotaxis cannot be determined in the full-grown buds ; the foliage leaves elongate tangentially and fold in a peculiar manner without increasing in radial depth to any extent after their first formation. As a consequence the curves soon become approximate Archimedean spirals so far as they can be judged by the eye ; but, as previously pointed out, it does not necessarily follow that such spirals of Archimedes imply *torsion*. The formation of special folded strap-shaped members is a secondary biological phenomenon which almost effectually masks the orthogonal system so far as it is visible at the apex.
>
> Thus, it is impossible to say from the direction of the spirals whether the three spirals seen are the complementary " spires " of a $(1+2)$ system or the three shorter curves of a $(2+3)$, since a left-hand genetic spiral would work out these same curves in either case. The interpretation taken, that the $(1+2)$ system is adopted, is based on the fact that two

members make contact round the axis, and the five "spires" of a $(2+3)$ system cannot be traced. The special type of folding may be regarded as the biological exaggeration of the "bean-like" form of the ovoid curve in a $(1+2)$ system. (*Cf. Mathematical Notes.*)

A similar spired appearance will also be secondarily produced in all types in which the numbers of the contact-parastichy ratio differ by unity: thus—

$(2+3)$	exhibit the complementary systems			$(1+\ 5)$	*Cereus* hybrids, seedlings.
$(3+4)$	,,	,,	,,	$(1+\ 7)$	*Sedum reflexum.*
$(4+5)$	,,	,,	,,	$(1+\ 9)$	*Cereus pasacana.*
					Lycopodium Selago.
$(5+6)$	,,	,,	,,	$(1+11)$	*Echinopsis*
					Zuccarinianus.
					Lycopodium Selago.
$(6+7)$	,,	,,	,,	$(1+13)$	*Echinopsis multiplex.*
$(7+8)$	,,	,,	,,	$(1+15)$	*Echinopsis Eyriesii.*

so that, while the parastichies may be readily counted, the one curve of the secondary system becomes the ontogenetic spiral, while the log. spiral "orthostichies" orthogonal to this curve form the respective number of "spires" (fig. 63, $(6+7)$).

Such types are best seen in the Cactaceae, where the latter curves are frequently emphasised by a biological production of ridges along their course; the primary parastichies are then counted by taking members in succession along adjacent ridges; the secondary curve which gives the genetic spiral, along alternate ridges, forming an obvious spiral winding around the apex of the plant.

Examples of the seven-spired type occur in vegetative shoots of *Sedum reflexum* and *Euphorbia biglandulosa*, in which a $(3+4)$ system occurs as a specific variation; in the former, the reproductive shoots assume the symmetrical constructions $(8+8)$ and $(6+6)$, while in the latter a normal *Cyathium* is produced.

The seven-spired effect produced in the $(3+4)$ system of *Sedum reflexum* (fig. 76), and *Euphorbia biglandulosa* (fig. 77), as also the five-spired system of $(2+3)$ *Euphorbia myrsinites*, is directly comparable with the three-spired screw of *Pandanus*, the special formation of the last case being intensified by the condensation

PLATE XV.

Fig. 57b.—*Gasteria carinata*, Haw. Asymmetrical, 2-spired, 20 cm. diameter.

Fig. 57a.—*Gasteria obtusifolia*, Haw. Whole plant 26 cm. across, symmetrical (1 + 1).

PLATE XVI.

Fig. 58b.—*Gasteria obliqua*, Haw. 3 seedlings, one asymmetrical. 12 cm. across.

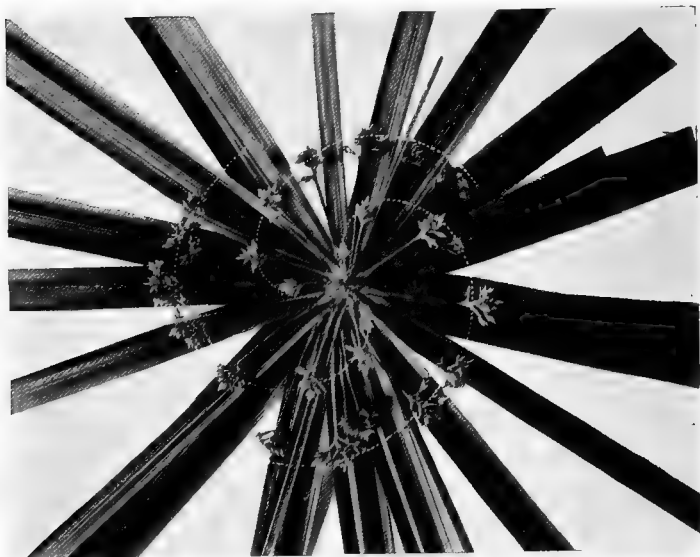Fig. 58a.—*Gasteria fasciata*, Haw. Asymmetrical. 2-spired. 30 cm. diameter

PLATE XVII.

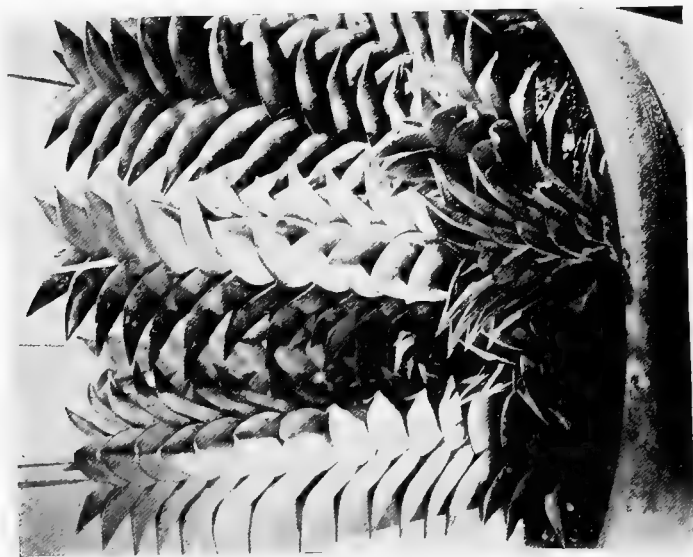Fig. 59b.—*Cyperus alternifolius.* Apex of fertile shoot, November.

Fig. 59a.—*Apicra spiralis.* 3-spired plants.

of the axis and the imbrication of the stout folded leaves. A similar condensation in the case of *E. biglandulosa* would produce equally good screw twists (fig. 77*b*), while an identical exaggerated spiral is seen in the winter-shoots of *S. reflexum* (fig. 76*b*).

Apicra spiralis, most commonly a five-spired form, $(2+3)$, varies to the three-spired form $(1+2)$, and is then very similar to *Cyperus* and *Pandanus*; owing to the greater succulence of the leaves, however, the system appears less telescoped, and the spiral twist less striking (fig. 59*a*). Section of the apex shows the same phenomena as those figured for the three-spired *Cyperus*. *Pandanus* is also identical.

Other good examples of such constructions are afforded by the shoots of *Lycopodium Selago* $(4+5)$, $(5+6)$ (fig. 78), where they occur in conjunction with true whorled systems $(3+3)$, $(4+4)$, $(5+5)$ (figs. 79, 80).

The production of "spired" types is of special interest in that in several cases the spires are extremely well-marked (*Pandanus*), and from their approximation to helices have been made the chosen examples of torsion theories. As previously noted, the appearance of Archimedean spirals, or true helices in the case of cylindrical axes, will only be produced when the members attain accurately equal bulk; *i.e.*, when they definitely cease further growth on reaching a certain specific volume. In such cases the "orthostichy" curves become straight lines; but so long as any *growth* is taking place, however little it may be, the similar members will retain the gradated series in which they were formed, although the difference between adjacent members, consequent on the retarded rate of growth, may be so small as to be inappreciable to the eye.

Ultimate appearances are complicated by the fact that cessation of growth may take place in two ways: either, as in typical and theoretically uniform leaf production over a considerable length of axis, members grow to a certain size and then stop; or, growth may diminish and cease uniformly throughout the whole system, with the result that the completed system retains to a very considerable degree the graduated sequence of its ontogeny; this being well seen in seasonal cessation of growth, as in the production

L

of buds and similar arrested systems, of which the Pine-cone affords a good illustration.

In the first-mentioned case the resultant curves will be spirals of Archimedes or helices; in the latter, modified logarithmic spirals, which may be conveniently described as "retardation spirals."

In the former case, again, the visible result will be the straightening out of the " orthostichy lines," and the spires of a spired system may thus become ultimately quite straight, such an effect being well marked in typical Cacti whose seedlings have obvious spiral ridges. The consideration of such growth-forms as these also illustrates the fact that the final effect is due not only to the assumption of equal volume in the members themselves, but also to the attainment of equal length in the secondary zones of elongation which constitute the internodes. So long, therefore, as the internodes are growing, the same appearance as that presented by a gradated series of members will be maintained, even when these members are practically equal. The spires of *Euphorbia biglandulosa* (fig. 77), and *Sedum reflexum* (fig. 76), thus continue to be well marked after the leaves have reached the adult condition owing to continued growth in the main axis. In the limit, the rows become much straighter, but usually only after the fall of the leaves. The " orthostichy " lines thus appear to become straighter and straighter, as growth slows down in successive members and internodes; but they will always be spiral lines so long as growth continues throughout the whole system.

Spiral " orthostichy lines " and " spires " are thus usually more obvious in buds and bud-sections than in adult structures, as originally noted by Bonnet; while if the whole system stops growth simultaneously these spiral orthostichy lines or spires become fixed, and the resulting structure has the appearance of a permanent bud.

In such a construction the secondary phenomenon of *dorsiventrality* produces very striking results. Thus the fact that a leaf increases tangentially to a greater degree than in radial extent may be regarded as due to a diminished radial rate of growth. Without going into further detail at present with regard to such a

standpoint, it may be noted that the effect of progressive dorsiventrality in a growing system will be to *exaggerate the curvatures* of all the spiral paths.   Thus the attainment of a degree of dorsiventrality sufficient to make a member about twice as broad as thick, as in the leaves of *Abies*, etc., will result in the fact that the " orthostichy " lines or " spires " become as curved as the shorter paths of the normal curve tracing, while these latter become as markedly curved as the normal longer paths.   With a still greater degree of dorsiventrality the spires become still further pronounced, so long, that is to say, as the system is either still growing, or else has stopped altogether.

The difficulty in the case of *Cyperus* and *Pandanus* is, however, not to prove that the curvature of the so-called " orthostichies," which is sufficiently clear in a section of the apex, may be due to *torsion*,* since in theoretical construction they should be curved and not straight; the question is why, with so great an assumption of dorsiventrality, these lines are not much more curved?   This may be possibly very largely due to the special mode of folding the strap-shaped leaves into one another; as they grow they slip over each other in such a way that they must form three rows in the bud, and the assumption of a divergence angle of 120°–126° (Schwendener) may be thus quite secondary.   For example, in *Cyperus* (fig. 51), the last leaves being rudimentary do not fold, and in a section cut apparently quite transversely the divergence angle between 6 and 7 was 134°; beyond these members the angles vary owing to change of system, while other irregularities are observable in the last folded members.   There is no real necessity to postulate torsion, nor is there any ready method of proving it.

So great is the alteration in such systems owing to the effects of rapid retardation in the rate of growth behind the apex, that the log. spiral construction, founded on theoretical uniform growth, completely fails to represent the results attained in the plant. One fact alone remains clear: in a construction in which growth is rapidly slowing down, and the members acquiring approximately equal radial depth, but still elongating tangentially, the appearance

* For torsion theory *cf.* Schwendener, *Botanische Mittheilungen*, vol. i. p. 163,

of Archimedean spirals will be subjectively produced, and the
orthostichy lines thus appear as if they ought to be straight. But
until such radial equality is produced the curves cannot be spirals
of Archimedes, and the "orthostichies" cannot be straight, what-
ever else the nature of the spiral may be. The assumption that
the orthostichies should be primarily straight thus entirely falls
to the ground, and torsion theories based on such hypotheses are
unnecessary.

VI. Symmetrical Non-concentrated Type.

LIKE the preceding, a comparatively rare formation, this forms the system known as *superposed whorls*.

Similarly, also, it is more general as expressed in terms of cells, than of lateral members of more massive character, being, in fact, the conceivably theoretical case for the primary arrangement of isodiametric cells in the growing points of all Phanerogams, and well seen in the unmodified tissues of many roots (*cf. Zea*). The remarkable absence of concentration systems in cell-tissues, while these form the characteristic feature of the arrangement of massive primordia, affords confirmation of the hypothesis that concentration is always derived secondarily through a spiral construction.   The presence of superposed whorls in the vegetative shoot is doubtful, but in floral mechanisms it is more general, and in a large number of cases generally accepted as being of secondary origin.   From the standpoint of the theory of Schimper and Braun, superposition of the members of successive whorls naturally followed from their constructions for superposed spiral cycles, and any deviation from such superposition had to be accounted for by prosenthesis.   The present standpoint, that alternation is the normal and primitive condition, thus renders many phylogenetic generalisations improbable.   The fact that in higher plants, whorled types appear to be always reached *viâ* a concentrated asymmetrical construction, suggests, therefore, that true superposition is always secondary.   The logical consequences of such a view have an important bearing on the structure of floral organs.   It becomes necessary to distinguish

between superposition which is mathematically accurate and that which is only apparent to the eye.

The determination of phyllotaxis systems in flower-shoots in which the construction is not continued for a sufficient number of members to judge whether the apparent orthostichies are truly vertical or really spiral, may present a difficulty.

Thus, spiral flowers may be constructed in the systems $(1+2)$, $(2+3)$, $(3+5)$, giving respectively cycles of 3, 5, or 8 apparently superposed members, on the lines of the three-spired *Cyperus*, five-spired *Apicra*, or an eight-ridged *Cactus* or *Euphorbia melo-formis*.

If the number of members is few, and their relative bulk very nearly equal, superposition may be sufficiently accurate to the eye, or may actually become so by secondary growth changes, as possibly in the flowers of *Beta* and *Amaranthus* with superposed perianth and androecium.

Thus the five-spired terminal flower of *Berberis vulgaris* presents cycles sufficiently superposed to the eye in the expanded flower, but in development the spires are better marked, so that the first-formed sepals would not be said to be at all superposed to the petals : the construction being, in fact, as markedly $(3+5)$ as in the case of *Delphinium Ajacis*. Similarly in *Nigella damascena*, in which the androecium is constructed in a $(5+8)$ system, the eight shorter curves, which are well marked in the expanded flower, have been interpreted as "oblique orthostichies."

On the other hand, mathematical superposition can only be produced in a symmetrical construction in which circles and straight lines really are present as the orthogonal construction paths of the system, and in such cases the superposition takes place between members of alternate whorls, the construction being that of a concentrated system.

Again, when some of the floral members show true alternation and others do not (*Ruta, Primula*), some secondary change must be implied; the presence of $(5+5)$ formation in part shows that at one time the essential organs of the flower must have attained this symmetrical construction throughout, and a definite stand-point is thus opened up for the consideration of obdiplostemony,

for example. In all cases, the correct solution can only be deduced from the observation of the contact-parastichies in actual development; but it becomes increasingly evident that the extension to the flower of the hypothesis that lateral members are primarily produced in a mechanical system and subsequently adapted to their special functions affords a satisfactory since well-defined basis on which to establish theories of the morphology and phylogeny of floral-structures.

VII. Multijugate Types.

WHEN the type of normal asymmetrical phyllotaxis is thus completely isolated as consisting of systems mapped out by log. spiral curves in the ràtio series of Braun and Fibonacci, 2, 3, 5, 8, etc.; and the type of normal symmetrical phyllotaxis is equally clearly delimited as a secondary construction, physiologically independent of the ratio-series, though connected with it phylogenetically, the greatest interest attaches to all other phyllotaxis phenomena, which though less common, may throw light on the causes which tend to induce symmetry, before postulating, as a last resource, some hypothetical inherent tendency in the protoplasm itself.

These types may be included under two series: firstly, the multijugate systems of Bravais; and secondly, systems in which the parastichy ratios belong to series other than that of Braun and Fibonacci, e.g., the 3, 4, 7, 11 . . . ., 4, 5, 9, 14 . . . ., or still higher series.

The term *multijugate* was applied by the brothers Bravais to types of phyllotaxis in which the numbers expressing the parastichy ratios are divisible by a common factor; so that $2 \ (13+21)=(26+42)$, a bijugate system; while $3 \ (13+21)=(39+63)$ would be a trijugate one.

Expressed in angular measure, there is clearly no difference between such divergences and the expression $\frac{1}{2}\frac{3}{1}$, and in the spiral theory of Schimper there was in fact no room for such types, except as anomalous expressions of transitional whorled stages or "*twisted whorls*" of 2, 3, etc., in which successive whorls were neither superposed nor exactly alternating.* The simple method

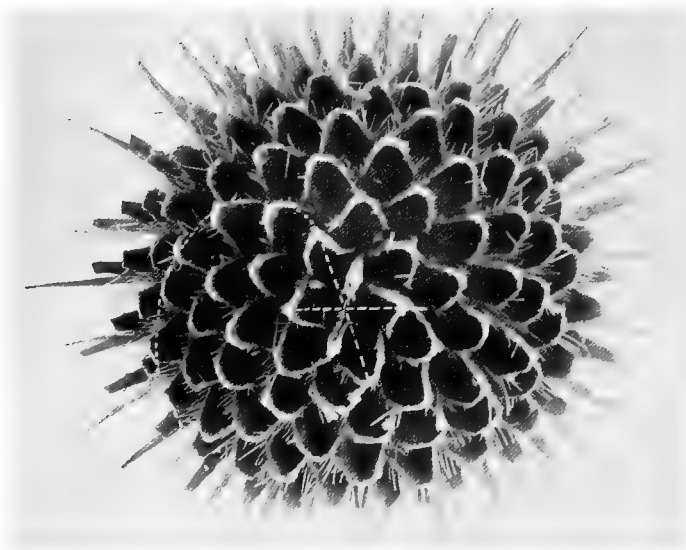* *Cf.* Wydler, *Flora*, 1851, p. 125.

PLATE XVIII.

FIG. 60b.—*Dipsacus pilosus*, L.   Inflorescence of the type
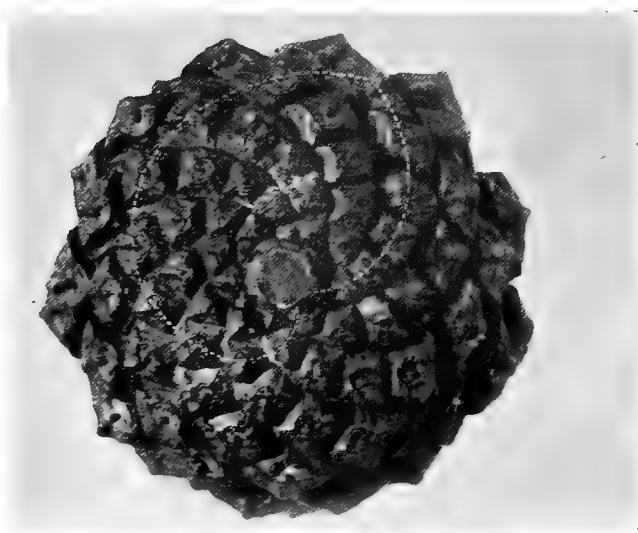10/16.

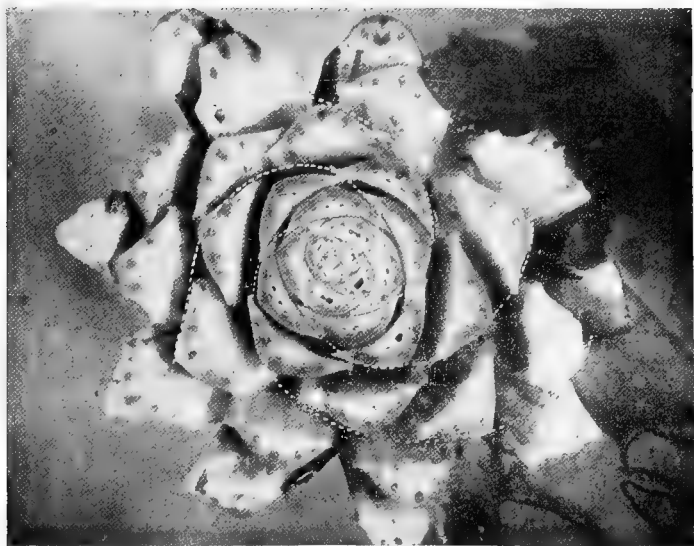FIG. 60a.—*Pinus pumilio*, bijugate cone of the type
6/10/16.

PLATE XIX.

FIG. 61b.—*Dipsacus sylvestris*, L. Seedling rosette (2 + 4).

FIG. 61a.—*Dipsacus fullonum*, L. Perennating plant cut across (2 + 4).

of regarding them as derived from two or more concurrent genetic spirals did not suit the spiral theory, which demanded one spiral line of growth.

Such forms of phyllotaxis are, however, not so rare as supporters of the Schimper-Braun hypothesis incline to suppose; they may occur in all types in which anomalous series are met with, and are most widely distributed.

They were first fully described by Bravais (*loc. cit.*, p. 96), although examples had previously been noted by Schimper and Braun, and also by De Candolle,* instances being observed in the inflorescences of *Dipsacus, Scabiosa, Arnica, Zinnia, Spilanthus, Piper, Veronica, Verbena*; flowers of *Cactus, Calycanthus*; cones of *Pinus maritima*, and foliage shoots of *P. palustris*.

The possibility of an approach to bijugate capitula in Composites is further shown by secondary maxima on the variation curves of Ludwig; while Weisse, out of a batch of 140 plants of *Helianthus*, obtained one bijugate example $(16 + 26)$.

The fact that they may occur in the plant which has already been found to exhibit normal phyllotaxis phenomena most completely, lends additional interest to these constructions. Thus, out of a batch of capitula, collected at haphazard by E. G. Broome, two were bijugate, $(26 + 42)$ and $(42 + 68)$ respectively; the others were quite normal; † while out of the total crop of 130 cones on a plant of *Pinus pumilo* (B. G. O., 1900), one cone only was $(6/10/16)$, fig. 60a, the rest being normal $(5/8/13)$.

The bractless spadices of Aroids have already been noted as presenting anomalous types of phyllotaxis, and among six inflorescences growing on the same plant of *Anthurium Crassinervium*, the parastichies of three were $(8 + 13)$, a fourth one was irregular, the other two multijugate of the types $(6/12/18)$ and $(6/9/15)$ respectively.

* De Candolle, *Org. Veg.*, vol. i. p. 326, 1827. "Leaves opposite in spiral pairs" in *Globulea obvallata*, and also according to Roeper in *Ajuga genevensis*.

† A case of extreme reduction in *Helianthus annuus* is of interest :—A seed germinated in a crevice of a stone wall, four feet from the ground (B. G. O., 1901) and developed a small starved plant : the impoverished terminal capitulum produced 10 ray-florets and 28 disk-florets. The contact curves of these were only $(6 + 10)$ as taken from a section-drawing. The capitulum was thus bijugate, although the 2-3 foliage leaves beyond the primary decussating pairs were not.

Dipsacus fullonum, having been very fully investigated by Bravais, may be taken as a type of the bijugate condition. Seedlings flower in the second summer, and the plants usually die after fruiting; the seedlings of the first year form a tuft of leaves with a very definite spiral arrangement. In other species, *D. sylvestris, D. laciniatus,* a well-marked radical-rosette is produced, in the latter the aggregate of leaves being flattened out on the soil to form a rosette two feet in diameter, in which apparently no two leaves are superposed, and to all appearances the spiral construction is that of the normal series (fig. 61*b*). If the plant be cut across (fig. 61*a*), the contact parastichies are seen to be well marked in the bud and constantly $(2+4)$; the first year's plant being thus bijugate as a seedling without any apparent reason.

In the second year a tall leafy shoot is sent up which bears leaves of the specialised " bucket " type, most marked in *D. laciniatus*; this shoot is at first sight symmetrical with " *decussate* " phyllotaxis, and beyond the vegetative leaves the apex produces a complex terminal capitulum which in well-nourished plants is practically constantly bijugate of the type $(26+42)$.

Thus Bravais found this type in 272 out of 350 capitula, or over 77 per cent. In the progressively smaller lateral heads, other systems appear, often trijugate, but sometimes of the normal series, and equally often anomalous systems or quite undeterminable types occur. Bravais tabulates 4 per cent. normal series, 4·5 trijugate, 7 per cent. undeterminable, and 6 per cent. anomalous systems. The facts, then, show that *Dipsacus* presents an example of a plant with a specialised leafy axis, springing from an asymmetrical system, and exhibiting, when the vegetative period is over, another asymmetrical system which, like the first, is normally bijugate.

The construction of a *Dipsacus* plant, then, is very remarkable if these facts are true,—that it commences with a $(2+4)$ rosette, becomes symmetrical (decussate) in the leafy shoot, and then produces a bijugate inflorescence $(26+42)$; since this would imply that a double transition from asymmetry to symmetry takes place in the life of the plant in passing firstly from leafy rosette to tall leafy shoot, and secondly, from inflorescence to flower. The assumption of symmetry in the floral members is so general that it

affords no difficulty. The "decussate" axis requires further investigation.

Examination of the rosette of a seedling (fig 62*a*, *Dipsacus sylvestris*) shows that the $(2+4)$ system is well defined, and results in the formation of alternating pairs of leaves in four spiral rows. By taking lines drawn through the centre of the median vascular bundles of each leaf on a drawing carefully made under the camera lucida, the angle at which the planes of successive pairs of leaves intersect may be measured with sufficient accuracy. That perfect accuracy is not attainable is shown by the fact that such lines do not intersect over the centre of the growing point; such disturbances being the effect of unequal growth, further evidence of which is seen in the drawing of *Scabiosa plumosa*, in which the spirals are not equally curved (fig 62*b*).

The angle measured in such a diagram averages $75°$ $(73°–77°)$; by constructing a log. spiral theoretical system of $(2+4)$ by means of log. spiral curves $(1:2)$, a similar system may be plotted out, and lines drawn similarly through the "centre of construction" of the "square" areas; on such a figure the theoretical divergence angle thus measured was found to approximate $73°$ (more correctly $72°$).

Observation of a *Dipsacus* plant which is commencing to send up an erect axis shows that the terminal bud maintains the same bijugate construction unchanged, and that the same system is continued in all the foliage leaves until the terminal inflorescence is produced. The leaves are therefore not decussate at all, alternating pairs crossing at about $72°$, and not at $90°$. True symmetry is thus never attained, the apparent decussation being due to a bijugate $(2+4)$ formation in which, owing to the fact that a bijugate construction implies two concurrent ontogenetic spirals, two members are produced at each node at points diametrically opposed.

The expansion of the system in the inflorescence is apparently not so accurate as the system deduced for *Helianthus*. Thus $(2+4)$ should normally expand to $(6+10)$, $(16+26)$, $(42+68)$, but *Dipsacus fullonum* gives terminal heads of the system $(26+42)$ as the type, and *D. pilosus* is even more constantly $(10+16)$ (fig. 60*b*). In noting this irregularity it may be pointed out that
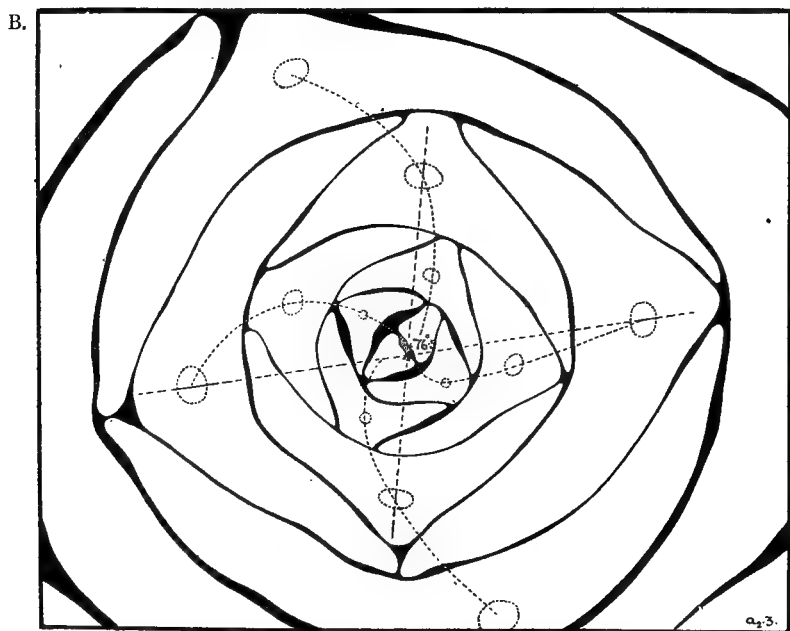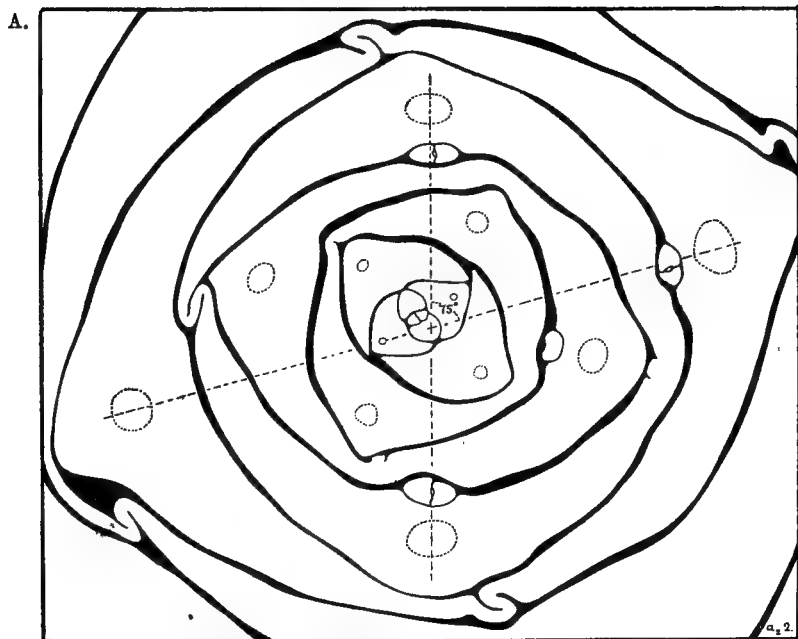
Fig. 62a.—Transverse section of a perennating seedling of *Dipsacus sylvestris* ; cam. lucid. drawing showing angle of oscillation of system (2+4).

Fig. 62b.—Transverse section of perennating shoot of *Scabiosa plumosa* ; cam. lucid.

while normal $(16+26)$ and $(42+68)$ have been already noticed in *Helianthus*, one capitulum was recorded as presenting the type $(26+42)$.*
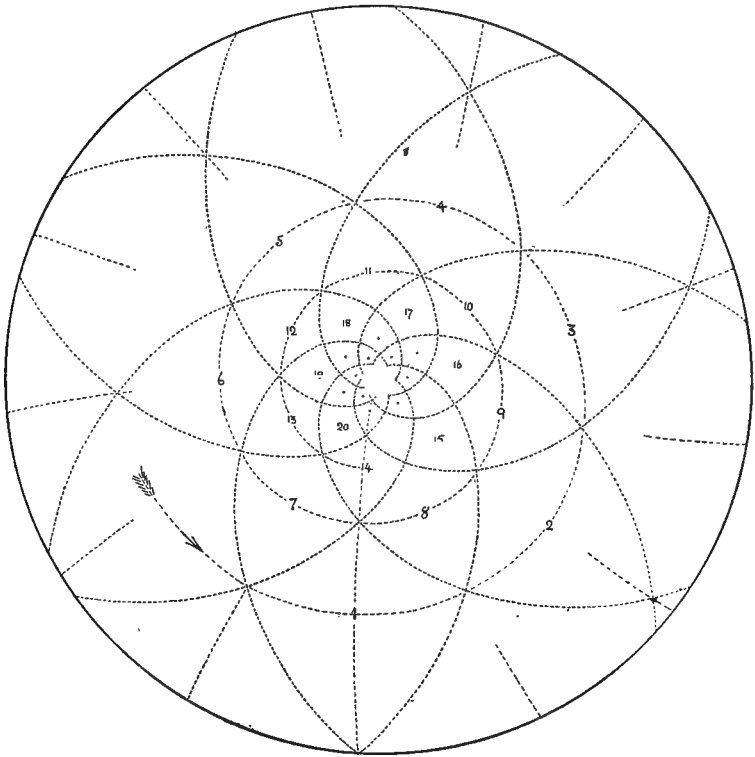
Fig. 63.—Geometrical construction for a system $(6+7)$ with complementry system $(1+13)$: *Echinopsis multiplex*, giving a 13-spired shoot with genetic spiral winding on apex.

As these anomalous capitula are rare in *Helianthus*, but the rule in *Dipsacus*, the section of the expanding series should prove of

* Such numbers being derived from observation of the external characters of the mature capitula, do not necessarily give the construction system, since if the facets observed subtend a smaller angle than the original primordia at their insertions, a higher series of curves will be apparent as the contact lines judged by the eye.

special interest. Owing to the subsequent tendency of *Dipsacus* to insert or lose curves on the main capitulum axis in order to compensate local growth variations, each capitulum requires to be taken on its own merits. The one selected suffices to indicate the normal procedure as well as the possibility and extent of local and individual variations.

Dipsacus fullonum (Anomalous Expansion System). A terminal head of a remarkably fine plant was taken at the end of March, when the inflorescence was just becoming visible among the leaves of the terminal bud. The plant had been growing fully exposed during a mild winter, and should have flowered in the preceding summer ; a series of hard frosts (22° F.) had also set in just as the head commenced to develop. Very little protection is afforded by the surrounding foliage leaves, and if external environment has any effect in producing anomalies, anomalous construction should be expected, and as a matter of fact it was very marked.

A section of such a capitulum (6 mm. in height), taken towards the lower part, includes the whole of the involucre, and may readily be drawn with considerable accuracy (fig. 64). Comparison of the involucral members shows two large median members (1 and 1'), and on the sides of the drawing 3 and 3', and 5 and 5', fairly clearly indicated, and diverging at something like the proper angle ; but careful measurement shows that the angle between 1 and 3 is only 60°, and that between 3 and 5, 70°. That a transition is in progress is obvious from the regular segmentation by ⊤-shaped walls, which might be easily mistaken for a tissue-drawing. This, again, is much clearer than in *Helianthus*, owing to the fact that the true primary members are here alone present and fill their rhombs, while the florets they subtend are only just commencing and have not as yet commenced to squeeze their bracts into the interstices between them.

The only modification of the theoretical orthogonal construction is found in the dorsiventrality of the members, which includes a slight normal slipping across the paths of the shorter curves. The leaf-pairs 1, 3, and 5 having been determined, it is easy, by approximating the divergence angle, to locate 7, 9, and 11. The three members 1, 11, 7 being in contact, it is clear that the phyllotaxis

of the capitulum commences as $(6+10)$, the normal expansion
derivative from the $(2+4)$ of the rosette and leafy axis.
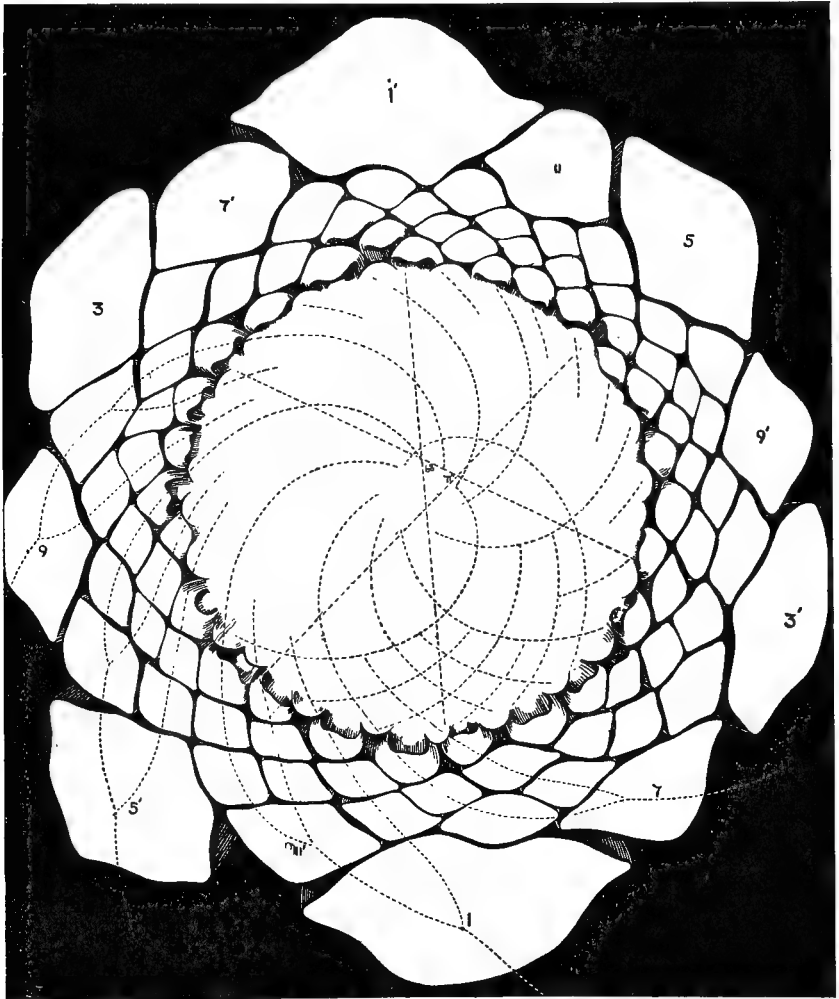
Fig. 64.—Section taken near the base of a young inflorescence of *Dipsacus fullonum*,
6 mm. long; cam. lucid. drawing; curve system up to point of section
$(23+24)$.

On counting the curves of the diagram, the remarkable fact is brought out that these are $(23+24)$ in the central portion of the system, with the possibility of further division in some of them. The anterior part of the figure shows clearly, however, the normal
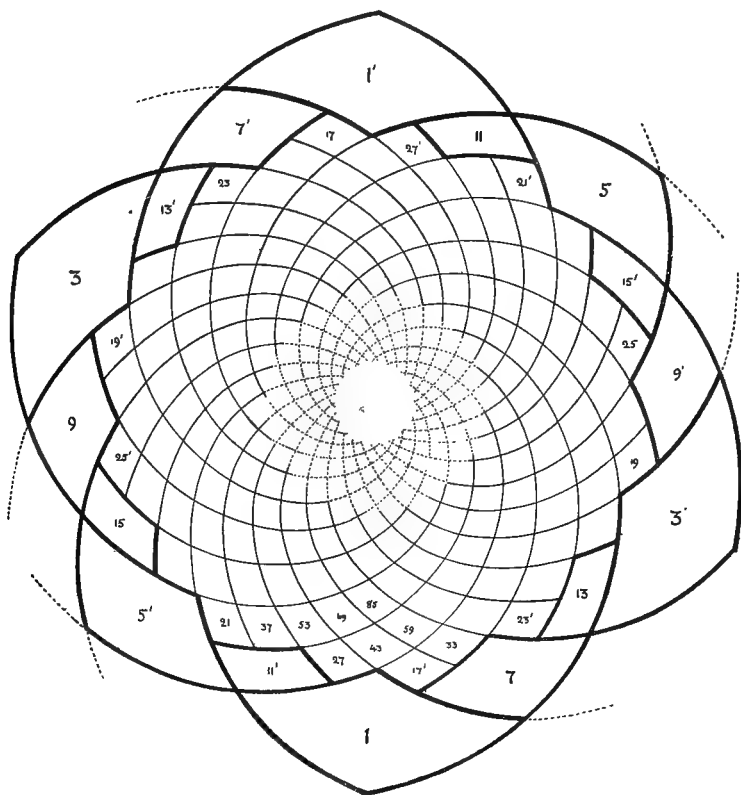
Fig. 65.—Theoretical curve construction for inflorescence of *Dipsacus fullonum*, $(16+26)$, as expansion derivative of $(6+10)$ continued from the $(2+4)$ of the vegetative shoot. A curve has been adopted which imitates the progressive dorsiventrality of the members.

appearance of a transition system (*cf. Helianthus*), which should therefore have been $(16+26)$.

It will therefore be an advantage if the $(16+26)$ system is constructed, and used as a means of comparison with this anomalous

system, so that the point at which error crept in may be located. A construction on lines similar to those used for *Helianthus* may be arranged ; a still closer approximation to the observed phenomena
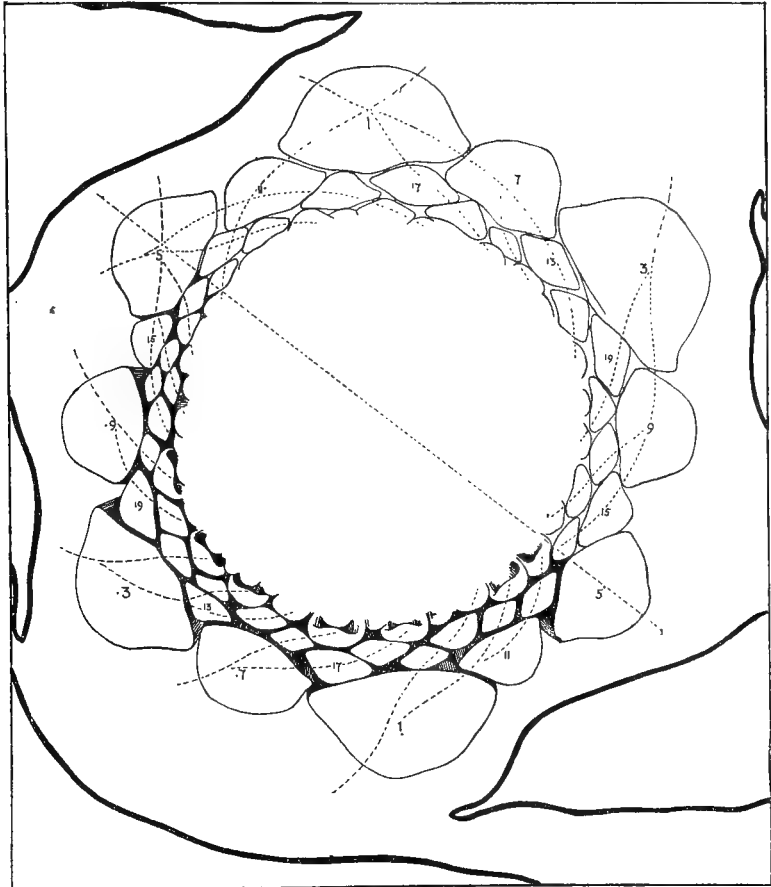
Fig. 66.—*Dipsacus fullonum.* Section of developing capitulum showing normal expansion (6 + 10) to (16 + 26) in agreement with the theoretical construction (genetic spiral reversed). On one side of a line drawn through 5 and 5′, the 3 long curves expand normally to 8 ; on the other side (shaded) 5 short curves become 3· 2· 3· 2· 3 = 13, the two halves of the bijugate system being inverted images of each other.

M

being obtained by using a transitional curve-tracing which expresses progressive dorsiventrality. The system would be theoretically mapped out by taking 16 long and 26 short curves in the ratio $8 : 13$; the ordinary $(3+5)$ curve being approximately accurate.

From the $(16+26)$ curves, the $(6+10)$ set are readily selected by taking paths in the system from No. 1 in the manner described for *Helianthus*; complexity coming in with the presence of two points of origin 1 and 1' (fig. 65).

The construction may now be compared with the section; segments 1, 3, 5 and 1', 3', 5' are clearly determined by these primary curves alone, and the transition commences with the pair 7 and 7'. Thus 7 and 7' each add a long curve, and 9 and 9' follow the same rule, with the result that at this moment the system is $(10+10)$; as in *Helianthus*, however, such transitional symmetry is ignored and the new curves go on being added. A difference, however, is now noticed, evidently due to the clashing of two Fibonacci series: 11 is bounded by two new curves, that is to say, adds one long and one short. The system is now $(12+12)$; similarly 13 adds two curves, and so does 15, the system thus maintaining symmetry at $(14+14)$ and $(16+16)$. Beyond this point, 17 adds one short curve only, and is followed by 19, 21, 23, and 25; the system again becoming asymmetrical and ending as $(16+26)$. The transition from $(6+10)$ to $(16+26)$ is thus effected on the diagram at the 26th member; but the first six did not enter this expanding series, but represent the members of transition from the previous $(2+4)$ foliage shoot.

The number of transitional members is thus apparently lower than in the normal series, *cf. Helianthus*, but agreement is shown in the fact that the outer 16 members which establish contact around the axis, constitute a species of protective involucre to the base of the inflorescence, and it is remarkable that their relative bulk is very approximately indicated by the area of the rhombs corresponding to them, a curious confirmation of the uniform character of growth in unspecialised members.

There can be little doubt but that this construction represents the actual distribution of growth in originating the inflorescence of *Dipsacus*, and any deviations from it must be regarded as

anomalies. It is now possible to consider the actual specimen (fig. 64) in relation to the theoretical scheme; this particular head $(23+24)$ represents a range of variation not included in the observations of the Bravais, and the $(16+26+42)$ type is fairly constant for strong terminal heads.

It will be noted that on tracing the ramifications of the long curves in the manner adopted for *Helianthus*, the areas leading from 1, 5 and 7, as also 1′, 5′ and 7′, correspond member for member, but not these leading from 3 and 9.

This is further seen to be due to the fact that 3 overlaps 7, instead of falling clear of it; so that 3 is possibly the member which has gone wrong, and the fact that the divergence angle between 1 and 3 was only 60° would be confirmed by the subsequent error of the system. New paths are being opened up from 9 as compensation at this point, but it appears that the construction has been thrown out by this displacement of one particular pair of leaves. To what extent such an effect might be ascribed to the action of the frosts at the time the capitulum was commencing is of course not evident from the consideration of one specimen alone.*

* It is clear, on the other hand, that too much importance must not be attached to the low divergence angle between 1 and 3, when it is borne in mind that these members are also contained in an expansion system derived from the $(2+4)$ of the vegetative shoot.

That the new $(16+26)$ system commences at 7, 7′, suggests that the $(6+10)$ system was only completed at 5, 5′, these members adding the last two short curves of the system. Allowing a new curve for each member, on the lines of *Helianthus*, this would imply that 1, 1′ added short curves, and four long curves were put in with the upper two pairs of foliage leaves : thus on a capitulum (fig. 66) which agreed with the postulated construction of fig. 65, the divergence between 1 and 3 was $59\frac{1}{2}°$, which agrees with the preceding within the limit of the error of observation.

It will also be noted that subsequent growth is not uniform : the members tend to come away from full contact, and a small amount of sliding growth accompanying the dorsiventrality must be allowed for. It is possible that the expansion from $(2+4)$ to $(6+10)$, as in the succeeding phase, is more rapid than the *Helianthus* type, since lateral capitula of *Dipsacus* show the inflorescence commencing immediately beyond the two vegetative prophylls. The case of the $(23+24)$ capitulum, granting a loss in the shorter curves, suggests that another expansion had commenced and added extra long curves beyond the type $(16+26)$.

Further discussion of these effects and the anomalies of a large series of such capitula would be beyond the range of the present paper, which only seeks to trace out the general lines of phyllotaxis as indicated by the homologies of cell-segmentation. Two points are specially striking in the expansion series of *Dipsacus*: first, the extent of the stations of symmetry in the expanding system, which subsequently give way to a renewal of the original ratio; and secondly, the beautiful approximation of the normal part of the diagram to the segmenting blocks of protoplasm characteristic of the tissues of many Algal forms (*Melobesia, Ralfsia, Coleochaete*).

In such a working mechanism, again, as in *Helianthus*, the genetic spiral is completely lost sight of and forgotten, although the two concurrent lines may be traced in numbering up the members; even the oscillation-theory is weakened, and the conclusion that the system grows and segments along new paths of distribution dependent on the pre-existing system, with the mathematical accuracy of the "crystallisation" of the Micellar Theory, is almost unavoidable.

Dipsacus thus presents an example of a plant in which the $(2+3)$ system of the Fibonacci series is replaced by $(2+4)$. This phenomenon, rare in *Helianthus*, here becomes the rule, and the whole construction of the main axis is bijugate. The reason for this is still wanting, but it is clear that what in *Helianthus* represents only an individual variation, is in *Dipsacus* a specific and even family character (*cf. Scabiosa, Cephalaria* *).

As will be described later, similar specific variations occur in anomalous series, as for example, the $(3+5)$ of *Sedum acre*, in contrast to the $(3+4)$ of *S. reflexum* (*cf.* figs. 76a, b).

That the true expansion type 16/26/42, given by the Bravais for the great majority of the capitula of *Dipsacus fullonum*, does actually obey the theoretical construction of fig. 65, is shown by a similar section of a developing capitulum in fig. 66; the agreement is perfect, and the addition of new curves is seen to follow the

---

* Variation to a true $(2+2)$ system was also found in *Cephalaria tartarica*; while the variation in one plant of *Dipsacus sylvestris* to $(3+6)$, giving "twisted-whorls" of 3, is of special interest in connection with the readiness with which $(2+2)$ is in some plants replaced by $(3+3)$.

3· 2· 3· 2· 3 law in the case of both the longer and shorter paths ; the two halves of the capitulum, on either side of any line drawn through one pair of members, are images the one of the other; while in this particular case, the whole diagram is taken as the reverse of fig. 65, as the two systems are useful for reference.

Identical constructions, tending to anomalous formations, occur in bijugate species of *Silphium* among the Compositae ; thus *S. perfoliatum* and *S. connatum* are wholly bijugate in their foliage shoots, and present the same pairs of "bucket" leaves as are characteristic of *Dipsacus*, while *S. laciniatum* obeys the normal Fibonacci ratios.

Silphium perfoliatum, L., normally produces terminal capitula which are bijugate of the same Dipsacus type (16+26) with variations. All subsequent lateral capitula of the inflorescence system, which goes on ramifying to the third degree in the type of a symmetrical dichasium (the ultimate ramifications being reduced as one prophyll alone remains fertile), are of the (13+21) type, and attain this phyllotaxis by progressive expansion from beyond the insertion of the fertile prophylls. The distinction between the bijugate and the normal capitula is obvious on looking at the involucre from behind ; the normal capitulum presenting a 3–5–8-star pattern, while the bijugate heads have four outer members arranged in a cross (fig. 67*b*).

These terminal capitula commence the bijugate character normally in the 2, 4, 6, 10, etc., series, but the construction subsequently becomes irregular : heads of *S. perfoliatum*, taken after the flowering-period (fig. 67*a*), show a remarkable similarity to the *Dipsacus* pattern of fig. 64 ; and a similar uniformity of growth in the leaf-members results in the fact that the transitional members become successively smaller in opposite pairs. The central portion is not clear, but the fact that irregularity may commence at an early stage is shown by the feeble development of 15, 15′, while 17, 17′ are still well-marked. Sections of such capitula, taken in the bud-stage, do not show the construction so clearly as in the case of *Dipsacus*; irregularity in the curve system is very marked, an average of 22–25 being observed among six capitula, and thus follows lines similar to those already described (fig. 64) ; the same addition of anomalous longer paths may be observed, and a similar loss of short curves ; the capitula do not, however, present so typical an appearance, owing (1) to the fact that dorsiventrality of the outer members is excessive, the four external members meeting round the axis, so that new contacts are established beyond those of the theoretical construction ; (2) the capitulum is almost plane, and the number of members inserted on it limited, hence the system commences to be destroyed almost as soon as the curve paths reach their maximum. Many capitula are thus rendered incapable of being counted.

The essential point to note is that the system commences regular expansion

as in *Dipsacus*, but in all the cases observed produced ultimately an anomalous and perfectly indefinite construction, the only point in common being the much closer approximation of the parastichy ratios to equality, so far as they could be estimated. On the other hand, the capitula in subsequent ramifications, right down to the smallest formed buds, appeared to be constantly $(13+21)$. There is so far, then, a distinct tendency for the first-formed and best-nourished capitula, to not only carry on the bijugate construction of the foliage-shoot, but to become further anomalous. It thus becomes of interest to compare allied species in order to see how far these irregularities are of local and individual or specific importance.

S. connatum, L., closely resembles *S. perfoliatum*, possesses the same "bucket-type" of paired leaves, as also the same general habit and size, but flowers about a month later. Of the terminal capitula, (B.G.O. 1901) some of the first-produced showed the bijugate 2, 4, 6, 10 pattern in the involucre, but the majority were of the normal $(13+21)$ type, as in the rest of the inflorescence. As the plants were growing side by side with *S. perfoliatum*, it is possible that a different period of flower-development may have had a local influence.

S. laciniatum, L., with normal asymmetrical phyllotaxis, has a more reduced inflorescence, while the size of the individual capitula is correspondingly increased. The terminal head of a strong shoot gave 34 short curves, but the longer were too irregular to count, although the approximation to equality was evidently very close ; a lateral head gave $(23+34)$, suggesting a slight rise beyond a $(21+34)$ system ; while the last formed heads presented $(21+34)$ exactly. It is thus clear that in *Silphium*, especially in leading capitula, the capacity for the addition of excess curves is very well marked, and the stations of the Fibonacci ratios are not observed under conditions of special nutrition with the accuracy of the normal plant for which *Helianthus* was regarded as a type. In other words, adopting the previous convention, the Fibonacci sense is less well-developed in *Silphium*, and anomalous constructions due to the interpolation of excess curves are readily produced ; but the tendency is again always towards a nearer approximation to symmetry, as exhibited by an approach to equality in the parastichy ratios. From these facts it is thus possible to argue that the irregularities in the particular capitulum of *Dipsacus* (fig. 64) were not due to the stimulus of external environment in the form of low temperature variations, but are to be correlated with the extra vigour in the main axis, due to the fact that the flowering period had been delayed. Once more, also, it may be pointed out how hopeless it is to express any of these irregular constructions in terms of "genetic-spirals," while they are readily discussed from the standpoint of parastichy ratios.

Similar relations between terminal bijugate inflorescences, which under excess nutrition tend to become anomalous, and lateral capitula of the normal Fibonacci character, are general among other members of the

Dipsaceae ; species of *Cephalaria* affording good illustrations. *C. tartarica*, Schrad., typically presents terminal capitula of the (10+16) type, and all the laterals (8+13) (fig. 68a, b) ; the appearance of these is sufficiently obvious in the bud-condition (fig. 69a), and the fact that the bijugate expansion commences normally is shown by fig. 69b ; specially fine terminal heads again show subsequent variations and irregularities. Similarly *C. radiata* gave (12+19) with slight irregularities for the terminal capitulum of a strong plant, (10+16) for all weaker ones, while all lateral (T′, T″) were (8+13).

C. leucantha, also terminals (T) (10+16), laterals (T′, T″) (8+13), and *Scabiosa atropurpurea*, terminals (10+16), or (6+10) in fruit, and laterals (8+13), becoming (5+8) in fruit.

In these plants, however, bijugate construction is only apparent in the terminal capitulum which closes a bijugate (2+4) vegetative shoot ; this type of asymmetry being lost in the lateral branches in which normal Fibonacci relations are restored beyond the prophylls. On the other hand, bijugate capitula occur in *Dipsacus* terminating branches of the first, second, and even third degree as well. The tabulation of the parastichy ratios observed in typical specimens of the commoner species will give the clearest idea of the distribution of multijugate, normal, and anomalous or irregular systems.

(1.) *Dipsacus sylvestris*, an average plant, 5 feet high, the terminal capitulum 95 mm. by 45 mm. in diameter, over the spines, showed an irregular construction about (30+33) at the broadest diameter ; * six other lateral capitula gave in order :—

$$
\textbf{T.} \qquad\qquad \textbf{T}'.
$$

$$
30+33 \text{ (irreg.)} \begin{cases} 27+36 \text{ (irreg.)} \\ 30+31 \text{ (irreg.)} \end{cases}
$$

$$
\begin{cases} 26+42 \\ 26+42 \end{cases}
$$

$$
\begin{cases} 23+28 \\ 24+36 \end{cases}
$$

Irregularity thus occurred in the leading capitula, and also in the last-formed basal ones ; two lateral capitula were exactly right, and all would appear to be derivates of the full 16, 26, 42 system.

(2.) A much finer plant, which had been growing in the open, 6 feet high,

---

* Note that in counting irregular systems, the eye is readily misled in following the wavy curves, and an approximation to equality in the ratios is thus often a consequence of confusion of two sets of parastichies. No data for such systems which are not taken from sections can be considered absolutely reliable.

with terminal capitulum 100 mm. by 50 mm. in diameter, and ten
lateral branches fertile, and thirty-five lateral capitula well developed,
gave :—

T.	T′.	T″.
$26+38 \begin{cases} 26+42 \\ 26+42 \end{cases}$		
	$\begin{cases} 26+42 \;.\\ 26+42 \;. \end{cases}$	$\begin{matrix} .\;\; 16+26 \\ .\;\; 16+26 \end{matrix}$
	$\begin{cases} 26+42 \\ 26+42 \;. \end{cases}$	$.\;\; 16+26$
	$\begin{cases} 27+44 \\ 25+42 \;. \end{cases}$	$\cdot \begin{cases} 16+26 \\ 18+29 \end{cases}$
	$\begin{cases} 26+40 \\ 26+41 \;. \end{cases}$	$.\;\; 16+26$
	$\begin{cases} 26+42 \\ 26+42 \;. \end{cases}$	$.\;\; 16+26$
	$\begin{cases} 26+42 \\ 26+42 \end{cases}$	$.\;\; 16+26$
	$\begin{cases} 26+42 \;.\\ \;\\ 26+42 \;. \end{cases}$	$\cdot \begin{cases} 16+26 \\ 21+31 \\ 16+26 \end{cases}$ $.\;\; 16+26$
	$\begin{cases} 26+42 \;.\\ 26+42 \end{cases}$	$.\;\; 20+31$
	$\begin{cases} 26+42 \;.\\ 26+42 \end{cases}$	$\begin{matrix} 16+26 \\ .\;\; 14+21 \end{matrix}$

The plant was thus remarkably constant throughout to the bijugate con-
struction ; in a few capitula, as counted at the broadest diameter, slight
irregularities occurred, but only four tertiary heads suggested a reversion
to normal (21+34). As previously noted, the difference between the
prominent sets of curves is due to the fact that the florets which are here
counted do not necessarily present the same contact-relations as the
primary leaf-members which subtend them.

(3.) *Dipsacus fullonum*, a strong plant grown in the open, 5 feet high ; the
terminal capitulum perfectly cylindrical and 100 mm. long by 40 mm. in
diameter, exhibited the type 16, 26, 42, unchanged throughout almost the
entire length of the capitulum : 14 lateral capitula gave :—

.

PLATE XX.
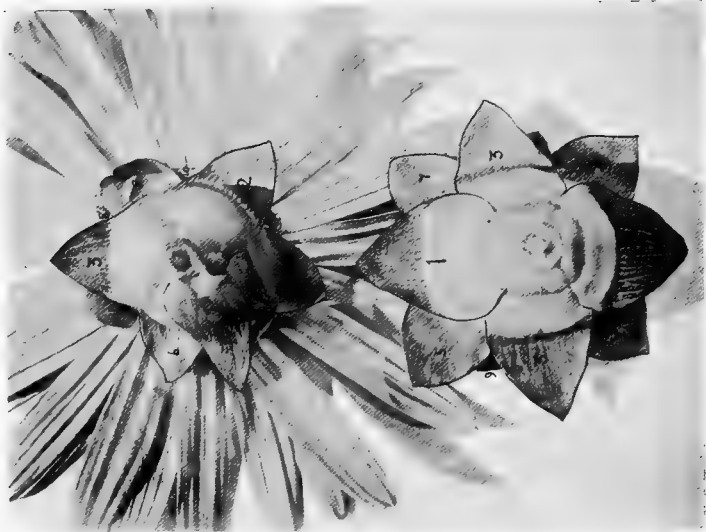
Fig. 67b.—*Silphium perfoliatum.* Comparison of terminal and lateral capitula from below; the involucral scales numbered.

Fig. 67a.—*Silphium perfoliatum*, L. Capitulum (terminal) after flowering; the involucral scales numbered for bijugate expansion.

PLATE XXI.

Fig., 68a.—*Cephalaria tartarica*, Schrad. Terminal
capitulum (10 + 16).

Fig., 68b.—*Cephalaria tartarica*. Lateral capitulum (8 + 13).

PLATE XXII.

Fig. 69b.—The terminal capitulum from below.

Fig. 69a.—*Cephalaria tatarica.* Young inflorescence of terminal and two lateral capitula, the former being bijugate.

T.	T′		T″.
16/26/42	$\begin{cases} (20+33) \\ \\ 16/26/42 \end{cases}$	. .	$\begin{cases} 8+13 \\ \text{malformed} \end{cases}$ $\begin{cases} 21 \text{ and irreg.} \\ 14+18 \text{ irreg.} \end{cases}$
	$\begin{cases} 16+26 \\ \\ 13+21 \end{cases}$	. .	$\begin{cases} 13+21 \\ 13+20 \end{cases}$ $\begin{cases} 13+21 \\ \text{undevl.} \end{cases}$
	$\begin{cases} 16+26 \\ \\ 16+26 \end{cases}$	. .	$\begin{cases} 13+21 \\ \text{undevl.} \end{cases}$ $\begin{cases} 16+26 \\ \text{undevl.} \end{cases}$

This plant thus showed a distinct tendency to revert to normal $(13+21)$ in the ultimate branches ; the irregularities are otherwise very slight.

(4.) *Dipsacus laciniatus*, an average plant grown in the open, 8 feet high ; the terminal capitulum, 100 mm. by 50 mm. over the spines, was irregular, the number of curves counted round the broadest diameter being $(26+38)$; 23 lateral capitula were borne on branches of the first, second, and third degree :—

T.	T′.	T″.	T‴.
$26+38$	$\begin{cases} 23+37 \\ \\ \\ 25+40 \end{cases}$	$\left\{\begin{array}{l} 16+26 \\ (20+31) \text{ (super.)} \\ 16+26 \end{array}\right.$ $\begin{cases} 18+31 \text{ (irreg.)} \\ 22+26 \text{ (irreg.)} \end{cases}$	$\begin{cases} 16+26 \\ 16+26 \end{cases}$ $\begin{cases} 13+21 \\ 16+25 \end{cases}$ $\begin{cases} 16+25 \\ 16+26 \end{cases}$
	$\begin{cases} 26+42 \\ 25+40 \end{cases}$	$\begin{array}{l} 16+26 \\ 17+24 \end{array}$	
	$\begin{cases} 21+34 \\ 22+31 \end{cases}$		
	$\begin{cases} 16+26 \\ 21+34 \end{cases}$	$\begin{array}{l} 16+26 \\ 17+26 \end{array}$	

Here also the constancy to the $(16+26)$ type is remarkable ; while individual irregularities are small, there is in several cases, apparently without rule, a marked reversion to capitula of the 13/21/34 series, and as in *D. sylvestris* the leading heads are more usually anomalous.

(5.) *Dipsacus pilosus*, a strong plant 7 feet high ; the terminal capitulum spherical and 50 mm. in diameter over the spines showed around its

greatest diameter a perfect (16+26) system. *D. pilosus* presents a more primitive type than the preceding species, in that the stem is branched freely to the third and fourth degree, and lateral branches continue the structure of the main axis, also retaining the bijugate construction. The capitula are smaller and contain relatively fewer flowers, the ultimate heads, in fact, often producing so few that the parastichies are too ill-defined to be counted.

The plant produces a multitude of small capitula instead of specialising a few large ones in the terminal region, and the type of construction is remarkably constant. Thus the plant selected, producing branches to the fourth degree from ten nodes, gave a total of 176 capitula sufficiently well developed to be counted : the last small heads remain undeveloped as the plant exhausts itself at the end of the summer.

Of the 175 lateral capitula, 112 were accurately (10+16) around the middle ; 30 were (6+10), the difference between these constructions being subject to secondary error in counting adult structures, 8 were only one or two curves out in either direction, and 25 were of the (8+13) type ; thus, in all, 80 per cent. were bijugate capitula, and about 15 per cent. reverted to the normal Fibonacci ratio.

The general phenomena of all *multijugate* systems can be readily studied from their structural diagrams, and though in many cases the systems are not necessarily constant for any considerable period, it is only by expressing the construction geometrically that the significance of a common factor to the ratio is made obvious. Thus a (10+16) system, characteristic of the inflorescence of *Dipsacus pilosus* and *Cephalaria tartarica* (fig. 68a), may be represented by drawing the 10 and 16 log. spirals in the requisite ratio 5 : 8 ; and since the mathematical fact that these curves plot the system is the only definite statement that can be made with regard to it, it follows that the system must be numbered by Braun's method, by taking members as differing by 10 and 16 along their respective paths : on so doing (fig. 70) it will be found that no interpretation in terms of "genetic-spirals" is possible save that which admits the presence of two equal and concurrent paths orientated at points diametrically opposed. Taking one of these as No. 1, the members are represented by odd numerals only, there are two Nos. 3, for example, but no No. 2, and by taking a divergence angle of 137° from 1, it will be found that each system has its own path 1, 3, 5, etc., and 1′, 3′, 5′, etc., and these "genetic-spirals" work out in a direction the reverse of that of a normal (5+8) system.

Other systems may be similarly constructed, and the essential point of the mathematical proposition rendered clear, that *in multijugate systems there is no longer a single genetic spiral.*

Such systems may now be viewed from the standpoint of a transition to symmetrical construction, in that while the Fibonacci

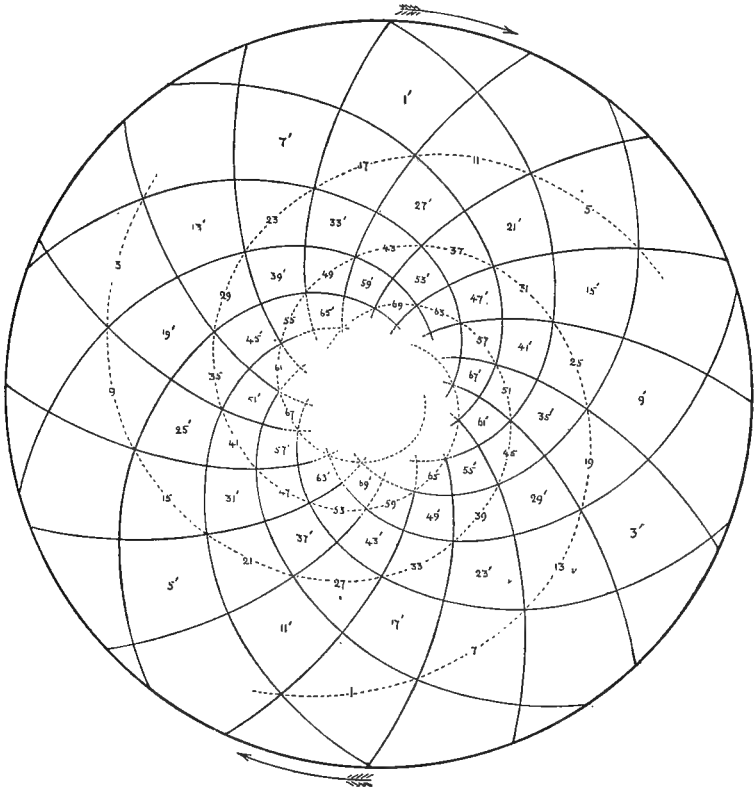
Fig. 70.—Geometrical construction for bijugate system (10 + 16).

ratios are to a certain extent retained, the construction is modified, with the result that two members are simultaneously produced, and the system, to continue a previous metaphor, is now built *two bricks at a time,* the members of each series being formed at the proper divergence angle. While again there is no nearer approach

to equality of the ratios, there is a distinct sign of symmetrical construction, in that any change involving a rise or fall in the system must, in order to retain the bijugate construction, take place by adding or losing two curves simultaneously, since if a single path be gained or lost, the ratio may become divisible by unity only and thus work out as a single genetic spiral.

From the point of view that a decussate system represents a doubled construction, $(2+2)=2\ (1+1)$, the possibility of the secondary reversion to the doubled spiral construction implied in bijugate systems is very apparent. The examples met with in the inflorescence of *Verbena* and the flower of *Calycanthus* might be thus explained; but it must be pointed out that the rule does not hold for *Helianthus annuus*, which, though decussate at first, reverts to normal Fibonacci ratios with almost perfect constancy; nor, again, does it apply to *H. rigidus* and *H. strumosus*, which are decussate almost to the terminal capitulum. The fact that the more obvious parastichies of garden *Verbenas* may vary from $(5+8)$ to $(6+10)$, and the floral members of *Calycanthus* in the same manner, is quite independent of the decussate phyllotaxis of the vegetative shoot, and comparable with similar variation in *Sedum elegans, Podocarpus japonica,* etc.

Again, the distinction between a truly decussate $(2+2)$ system and the bijugate variant $(2+4)$ is often indistinguishable to the eye, so far as the general appearance of the adult shoot is concerned. That very considerable displacements may take place in the former symmetrical construction is shown, for example, by taking sections of a decussate bud of *Epilobium angustifolium* (perennating shoot): on cutting a section a little above the actual apex (fig. 71, 1), very considerable changes may be seen to follow irregular growth and twisting of the older leaves. Such distortion is very general in decussate leafy shoots, and requires to be carefully separated from bijugate construction. Thus in the typically decussate family of the Labiatae, this external deformation of the symmetrical construction is very common, and the original case of *Ajuga genevensis* evidently comes under this head: in rosette - forming members of this and other families, or in their seedlings and perennating foliage shoots, the apparent reversion to an asymmetrical

system is often very marked. (*Dianthus, Phlomis* (fig. 73), *Urtica*, etc.)

These irregularities in petiole formation, etc., might evidently occur to an equal extent in asymmetrical systems, but they would
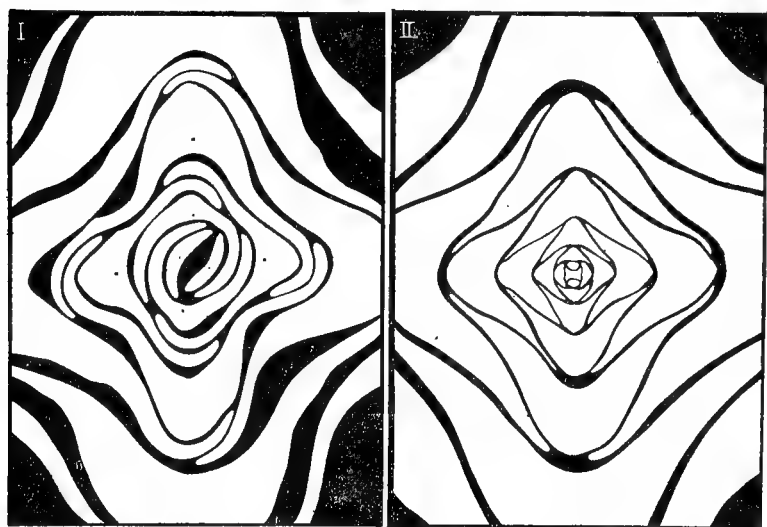
Fig. 71.—*Epilobium angustifolium*, L.—I., section some distance above the apex of a perennating shoot. II., section exactly at the apex, symmetrical (2 + 2) system.

not be so readily noticed, owing to the difficulty of judging the error of such constructions by the eye alone.*

* If two equal and similar leaf-primordia meet around an axis and tend to pack, the chances are that, if the ends are well developed and rounded, one will slip under the other on one side and over the other on the opposite side. The two developing members thus become pushed askew with regard to their true position and that of adjacent members, and an irregular effect is produced. To test true symmetry (2 + 2) as opposed to bijugate (2 + 4) construction, it is necessary to cut the primordia at the apex before they commence to overlap (fig. 71, 2). Again, such secondary confusion will be greater in a symmetrical construction where the primordia of the same whorl should exactly meet, since in the case of asymmetry the paths for slipping are provided in the spiral construction. Hence a symmetrical system tends to give greater secondary irregularity than an asymmetrical one, and it is thus rather the exception than the rule for a decussate plant to show four strict orthostichies. The externally visible

The multijugate systems, so far considered, have been either the $(2+4)$ system regarded as a variant of the $(2+3)$, or the cases, 6/10, 16/26/42, which represent the normal expansion along the lines already indicated for *Helianthus*.

More elaborate systems, divisible by 3, 4, etc., occur chiefly among the Cactaceae and similar growth-forms, as variations of anomalous systems which become divisible by common factors, and these will be noticed under the special heading.

Among bijugate types, two cases call for special mention; the $(6+10)$ of foliage shoots, and the expansion type $(10+16)$ which does not represent the normal sequence, but apparently indicates a stoppage at an intermediate stage in the normal Fibonacci expansions.

The $(6+10)$ appears to be initiated directly on vegetative shoots, in which it may be regarded as a variant, possibly often local, of the normal ratio $(5+8)$.

Thus *Pinus pumilio* cone, normal $(5+8)$, varied to $(6+10)$ (fig. 60a).

Sedum elegans shoots, vary $(5+8)$ and $(6+10)$ (fig. 43).

Pinus Pinea seedlings vary $(5+8)$ and $(6+10)$.

Podocarpus japonica leading shoots vary $(5+8)$ and $(6+10)$ (fig. 42).

In dealing with *Araucaria*, it has already been shown that from the standpoint of bulk-ratio, $(6+10)$ represents an intermediate stage approximating $4:1$ (or $3·8:1$), and is therefore equally possible as an alternative construction with $(7+11)$, which approximates $4:1$. The conclusion that $(6+10)$ may therefore represent an enlargement of a $(5+8)$ system, in which the bulk of the axis is increased without the lateral primordia taking their relative share in the increased nutrition, is unavoidable, and the manner in which $(6+10)$ is found associated with $(5+8)$ in the examples given strongly supports it; on the other hand it may be regarded with equal probability as the expression of an inherent

result depends on the extent to which the members more than fill their full arc or fail to do so. In the latter case four straight rows of narrow leaves are observed (*Euphorbia Lathyris*, 4-ridged *Cacti* and succulent *Euphorbiae*); in the former with broad or sheathing leaves the rows may be perfectly irregular (*Dianthus*).

variation capacity on the part of the plant, and entirely independent of circumstances of nutrition: experimental evidence may throw light on the point.

The $(10+16)$ type was found to be constant to a remarkable extent for lateral capitula of *Dipsacus pilosus*; such capitula are easily cut in early stages, and owing to the relative length of the spiny bracts, the whole of the system may be obtained in one section. As in other examples, growth is extremely uniform, and although the members lose their lateral contact except at their bases, they maintain their relative positions with great accuracy. A section of such a capitulum, taken near the base, shows unmistakably, however, that the contact edges of the rhomboid members lie along the paths $(16+26)$ (fig. 24, 2), and that the appearance of $(10+16)$ is therefore secondary, and due to the fact that in the adult head the curves are counted from the contact lines of florets rather than of the bracts. When these florets, which tend to be more constant in volume on capitula of different sizes, subtend a greater angle than the original member in whose axil they arose, it is clear that new contact lines will be emphasised and the system apparently altered. A similar result occurs in the elongated fruit-heads of *Scabiosa atropurpurea*, these in the flowering condition show most usually terminal heads $(10+16)$, and laterals $(8+13)$, as contact-lines for the florets which diminish in size towards the centre; in the fruit-head, owing to the greater development of the involucels, the more obvious curves reduce to $(6+10)$ and $(5+8)$, while the fact that the fruit must be all equal in bulk is correlated with an elongation of the axis and the tendency for the conversion of the curves into intersecting helices on a cylindrical surface.

A section of a similar capitulum of *D. pilosus*, taken at the insertion of the terminal members, is of further interest in that the fall of the bijugate system is shown to be absolutely regular, and the last two sterile members are diametrically opposed. The system, that is to say, remains bijugate to the end; this may be more strikingly demonstrated by numbering the members backwards; the contact paths will be seen to change from differences by two to six, and by four to ten, as perfectly as in the number-

ing of the expansion system of the involucral region (fig. 74, 1).

The terminal capitulum of *Cephalaria tartarica* may be taken as typical of a definite $(10+16)$ system. The vegetative shoot is normally $(2+4)$, as shown by the paired leaves, and the terminal head presents the six-parted pattern (fig. 75) characteristic of *Silphium*, etc., and is much flatter than that of *Dipsacus*. A section of such a capitulum may be taken in the bud condition, 8 mm. in diameter, just at the level of the insertion of the last formed bracts, to include every leaf on the head, owing to the close imbrication of the well-developed peripheral members. The subtending bracts are markedly dorsiventral, and the slight amount of sliding growth has operated normally, with the result that the longer paths become more pronounced; and where the florets are cut, the curves, as in *Helianthus*, approach the orthogonal construction more obviously owing to the similar character of the more or less circular florets. Such a section (fig. 75) affords a beautiful example of rising and falling phyllotaxis, and this particular capitulum shows a descending system with the accuracy of the diagram of *Dipsacus pilosus*, the terminal members being two sterile scales orientated in the same plane as the first involucral pair.

On such a diagram every leaf may be numbered by taking an approximate oscillation-angle of 137° from 1 and 1′, whichever end of the system be taken as a starting-point; the figure is thus numbered from the outer involucral scales 1 and 1′ to 137 and 137′, the capitulum thus including 136 members. Owing to the marked dorsiventrality of the members and slight sliding-growth across some of the curve-paths, it is not possible to accurately follow the interposition of new paths, according to the convention adopted in the previous cases of *Helianthus* and *Dipsacus*. The system, however, commences as $(2+4)$, and 3 and 3′ do not make complete contact, but open up room for 5 and 5′: thus according to the convention, each 5 may be said to add a new curve to the system. That the maximum attained is really $(10+16)$, as shown in the section, appears to be fully warranted by the comparison of other sections, although it is true that only the tips of the

PLATE XXIII.
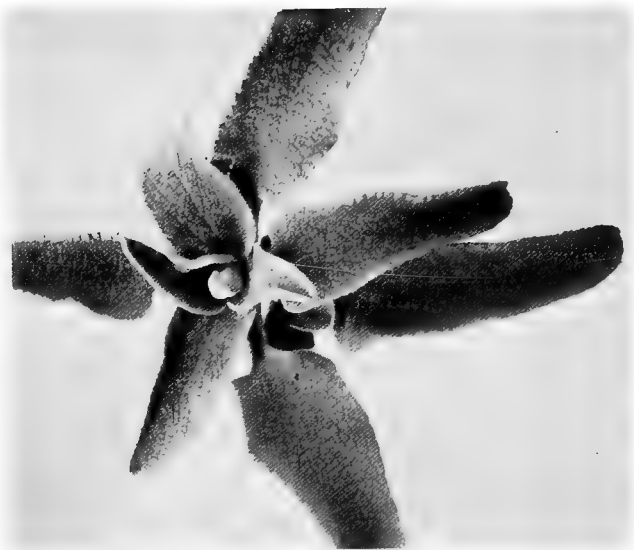
FIG. 73.—*Phlomis fruticosa*, L. Perennating shoot (2 + 2) with secondary distortion.
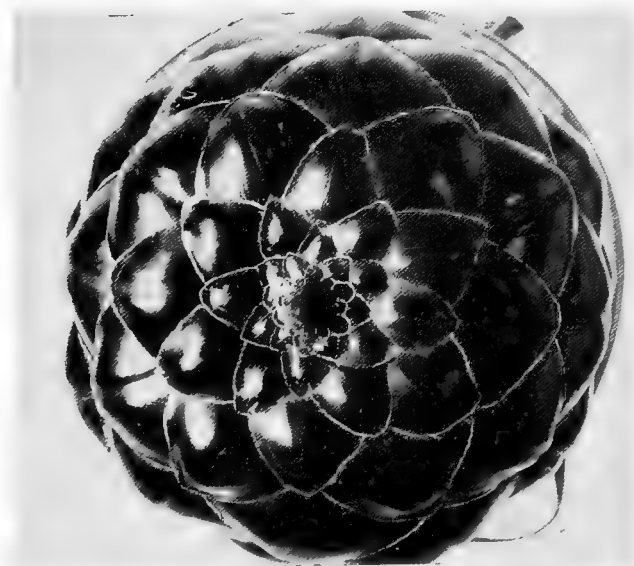
FIG. 72.—*Raphia Ruffia*, Mart. Symmetrical arrangement of scales on fruit (6 + 6).
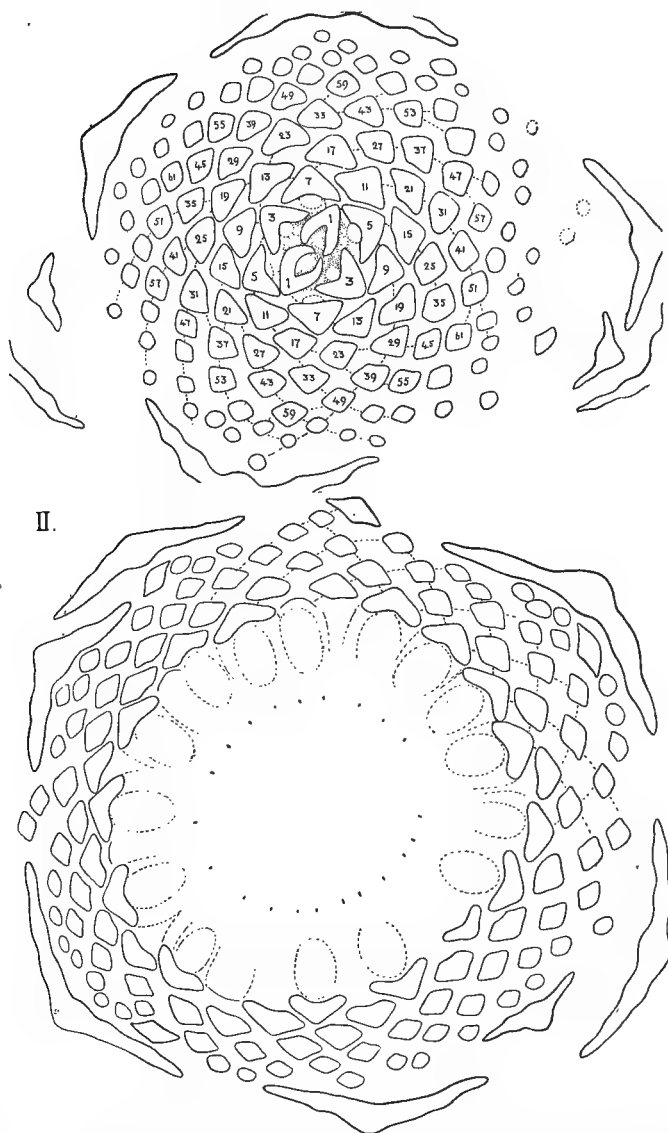
Fig. 74.—*Dipsacus pilosus.*—I., section of young capitulum at level of terminal members, numbered backwards as an expansion system. II., a similar capitulum cut near the base, showing contact parastichies (16 + 26).

majority of the members are cut, and the original construction does not necessarily follow from such a section. Taking the rise from $(2+4)$ to $(10+16)$ as the expression of the addition of 20

Fig. 75.—*Cephalaria tartarica*, Schrad. Section of terminal capitulum 6/10/16 type, numbered throughout.

new curves, the system should be complete at about twenty-six members, and this is possibly the case, but the proof is not definite:
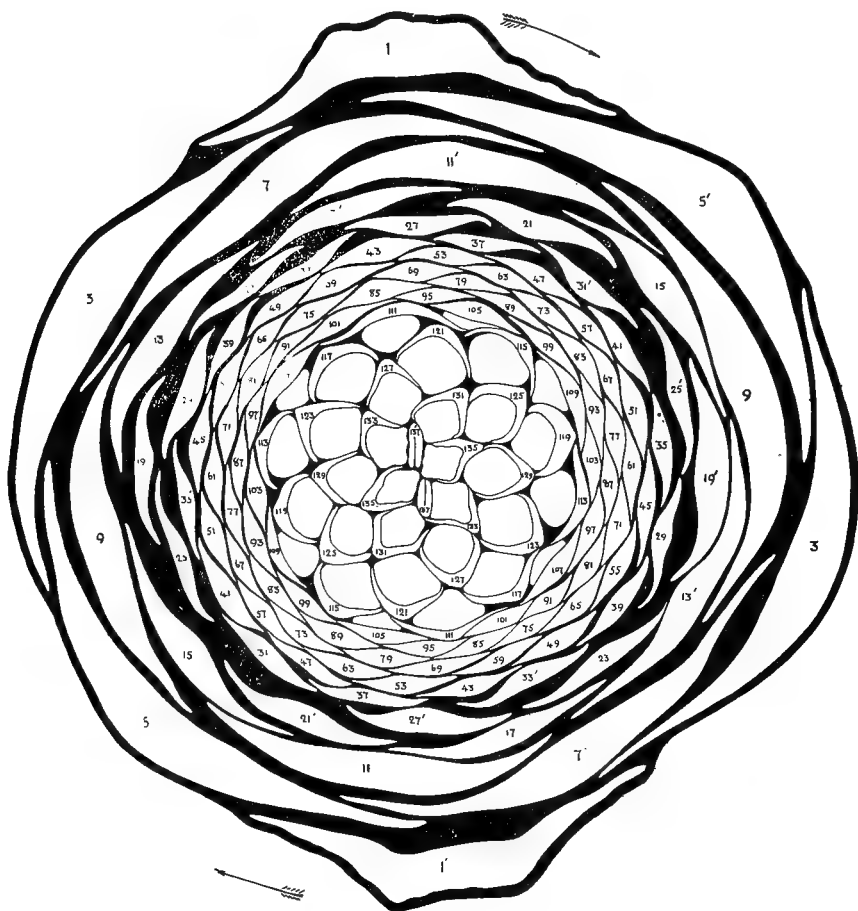
a fall apparently commences at about 101, and the curves are evidently dropped out with the regularity postulated for "discontinuous phyllotaxis" in the Fibonacci ratio.

Such a diagram presents, in fact, an elegant epitome of the phenomena which any theory of phyllotaxis is called upon to interpret, and if possible explain. It includes a bijugate construction, rising from a known constant system of $(2+4)$ to an equally definite $(10+16)$ system, as shown by the contact lines of the rhomboid members, and then falling equally symmetrically towards the close of the construction to two leaves placed opposite each other in the median line, just like the initial pair of the series.

Treated as the product of a spiral ontogenetic line of development, or an oscillating growth movement across the apex, laying down new growth-centres at an approximately equal divergence angle, it is clear that two such genetic paths must be in operation, producing members in diametrically opposed pairs, and that the adjustment of members with a progressively lowered bulk-ratio must also involve slight changes in the oscillation-angle, since the angle which builds a $(2+4)$ system is not the same as that which builds a $(10+16)$; how these angular changes may be controlled by the plant is at present quite inexplicable.

Treated, on the other hand, as a system in which new growth-centres are formed at the points of intersection of indefinitely continued asymmetrical construction curves, among which new paths may be opened up or subsequently closed according to a simple law for the spacing out of the added members around the axis, as already hypothecated for *Dipsacus*, the number of "genetic spirals" which work out the system in point of time, as also the exact oscillation-angle, becomes immaterial, and the subject admits of clearer expression and is easier to handle. Such a standpoint is here put forward solely on account of these reasons; it is sufficiently obvious that it does not follow that the simplest method of dealing with facts necessarily involves any account of their actual evolution or causation. To suggest that the plant knows what it is doing in laying down a stated number of curved paths is of course as futile

as was the original demand for a spiral line of growth as an expression of the plant *aim*.

Inherent asymmetrical growth entails the phenomena of a spiral system, and the number of the curved paths is determined by the mathematical claims of radial symmetry in construction, limited by the relative size of the new members. Individual or accidental variations on such a theme will produce more or less definite modifications; and such, if markedly beneficial, may no doubt become stereotyped as specific constants. There is so far no reason therefore why $(2+4)$ as a variant of a $(2+3)$ system should not be almost as common as the symmetrical $(2+2)$; it does not give the symmetry which protects lower leaves from vertical light, but it does give two opposite members which become localised at a node, and this in *Dipsacus* and *Silphium* (sp.) appears to be a definite biological advantage, although it is not apparent in *Scabiosa* and *Cephalaria*. Once given the $(2+4)$ system, the expansion derivatives follow rules as perfect as those deduced for *Helianthus* and *Cynara*, while the descending system is again the most perfect yet described.

The phenomena of multijugate systems thus indicate even more clearly than in the case of expansion systems and falling phyllotaxis of the normal series, the weakness of the " genetic-spiral " hypothesis as interpreting changes and variations either local or specific in asymmetrical construction.

How the asymmetrical system is actually originated in a shoot-apex is not yet apparent, but the conventional standpoint of bulk-ratio, in which a member is formed of a certain relative size at an approximately accurate divergence angle, so far summarises the facts. But once a working system is produced and the members of a full cycle laid down, it becomes increasingly clear that the subsequent history of the system is controlled much more by these existing curves than by any "spiral line of growth." New paths are added regularly according to the Fibonacci law, or quite irregularly, with the result that the numbers indicated by the contact-parastichies alone express the system, and if these happen to vary so as to be divisible by a common integral factor, multijugate systems result.

The method of regarding such systems as controlled by two or more genetic spirals neither presents any further explanation of the phenomena, nor is more generally useful in practice, than it would be if every parastichy line were called a genetic spiral, since all equally go on winding indefinitely. It is interesting to compare such a standpoint with the original conception of "Multiple Spirals" put forward by Bonnet and Calandrini.

VIII. Anomalous Series.

UNDER this heading may be included all ratios not divisible by
a common factor which are not included in the Fibonacci series.
The formation of imitation summation series has been previously
described, as for example :—

$$3, \quad 4, \quad 7, \quad 11, \quad 18, \quad 29, \quad 47 ;$$
$$4, \quad 5, \quad 9, \quad 14, \quad 23 ;$$
$$5, \quad 6, \ 11, \ 17, \ 28, \text{ etc.}$$

And it has been pointed out that such series differ from the
Fibonacci series in that the ratios of successive terms are neither
approximately constant, nor do they always approach $1 : 1.62$,
although this ratio is approached as the series proceed.

It has further been shown that the number of parastichy curves
is usually low, and it follows that among low numbers almost any
ratio must be capable of expression in one series or the other.
For example, in such a series as—

$$6 : \ 6$$
$$6 : \ 7$$
$$6 : \ 8$$
$$6 : \ 9$$
$$6 : 10$$

one system would be symmetrical,
two bijugate, one trijugate, and
one anomalous ;

and the close relation of such forms as variation types, is seen
among Cactaceae. (*Cf.* special section.)

But it does not follow that all the ratios of such hypothetical
series actually exist in plant structures.

For example, $(3+4)$ is found not uncommonly (*Sedum, Euphorbia,
Cereus*), and $(7+11)$ also occurs (*Araucaria*), but $(4+7)$ is very

rare. Similarly $(4+5)$, $(5+6)$ may be found in *Lycopodium* and *Cacti* as constants, but not the rest of the series; although their occurrence as transitional stages is not impossible (*Cacti*), the general rule which may be formulated at this stage of the consideration of anomalous series being, that any anomalous system represents an equal or a *nearer* approach to equality in the ratios than those of the normal series, and that their occurrence may be taken as a sign of a nearer approximation to symmetry.

The following cases may be considered separately :—

1. High ratios approximating equality and associated with symmetry.
2. High ratios produced as expansion systems.
3. Low ratios as specific or individual variations.
4. Production of anomalous systems by irregular introduction or loss of curves.
5. Acquisition of symmetry.

I. *High numbers the ratio of which is considerably nearer equality than the normal 1 : 1·62.*

That these represent variations on all but perfect attainment of the symmetrical condition is shown by the fact that they occur side by side with true whorled specimens.

For example :—*Acorus Calamus* commonly presents parastichies of the form $(15+15)$, but almost equally $(14+15)$ may be counted. *Echinops dahuricus*, often described as whorled in its inflorescence, shows parastichies very clearly on the almost spherical receptacle after the fall of flowers and fruit in autumn : five primary heads gave $(16+16)$, $(16+13)$, $(16+16)$, $(15+12)$, and $(15+13)$, while smaller lateral inflorescences only $(12+13)$ and $(13+13)$.

It is difficult to avoid the conclusion that these numbers represent slight deviations from a symmetrical construction based on an asymmetrical system $(10+16)$ or $(8+13)$.

The scales on the fruits of *Raphia Ruffia*, again, vary between $(6+6)$, $(6+7)$, $(7+7)$ and $(6+8)$ on the same inflorescence, fig. 72, $(6+6)$.

It is of interest to note that in these cases the question of normal phyllotaxis is entirely put on one side. In the two first, the primary members are, so far as is visible, ontogenetically absent, and the secondary radial floral axes cannot be expected to necessarily follow identical laws; while in the last, the lateral members are emer-

gencies more or less symmetrically placed on a foliar structure which only resembles a shoot in that the aggregated carpels constitute a mass exhibiting radial symmetry.

II. *Higher members of the series 3, 4, 7, etc., and 4, 5, 9, etc.*

Examples of such constructions occur in *Dipsacus* and *Helianthus*, side by side with bijugate representatives, and clearly represent in the latter the expansion-series of seedling variations.

As pointed out by Bravais (*loc. cit.*, p. 100), great care is required in the case of *Dipsacus* in which single curves are readily dropped or added in the middle of the inflorescence (figs. 38*a*, *b*), and the ratios derived from the number of parastichies will often vary in the different portions of the head. Many examples are given by Bravais; thus a capitulum presenting $(23 + 37)$ would be a member of the 1, 4, 5 . . . . series, but the omission of one curve in either direction, by reducing the system to $(22 + 36)$, would cause it to be included under a bijugate construction of the 1, 3, 4 . . . . series.

In the case of *Helianthus* the curved systems acquire a greater degree of constancy, and the ratios, with rare exceptions, are perfectly definite. Thus Weisse obtained one bijugate and six anomalous capitula of the types $(18 + 29)$ and $(47 + 76)$ among 140 plants. Although Weisse's pot-plants were obviously very poorly nourished, the percentage of anomalous capitula was no greater than in plants grown in the open, so that it does not appear that such anomalies are directly induced by bad environment. As previously noted, two bijugate capitula were found among a batch of 15 from one garden, while another batch of 15 plants, grown under the most unfavourable conditions (B. G. O., 1900), included three anomalous heads (29 $+ 47$) and $(47 + 76)$, as well as one which could not be counted at all.* From the point of view that variations are initiated in the seedling, these results would not be surprising, and they would seem to imply that the expansion series proceeded normally in spite of bad environment. That these constructions are not merely due to

* Pot plants were placed in an open bed late in June, and remained without water throughout the whole of a dry hot season. They grew about 3 feet high and produced capitula which only began to expand early in November, when they were all cut down by a hard frost. The remaining twelve were half $(34 + 55)$, the others $(55 + 89)$.
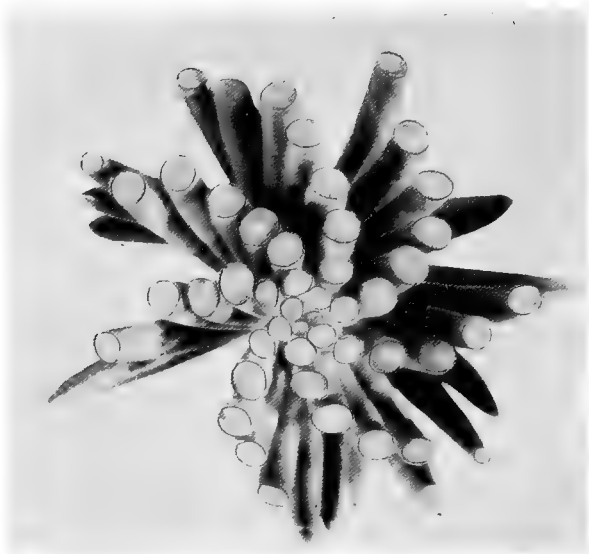
PLATE XXIV.

Fig. 76b.—The same shoot cut transversely, slightly magnified.

Fig. 76a.—Sedum reflexum, L.   Foliage shoot (3 + 4) = 7-spired.

PLATE XXV.
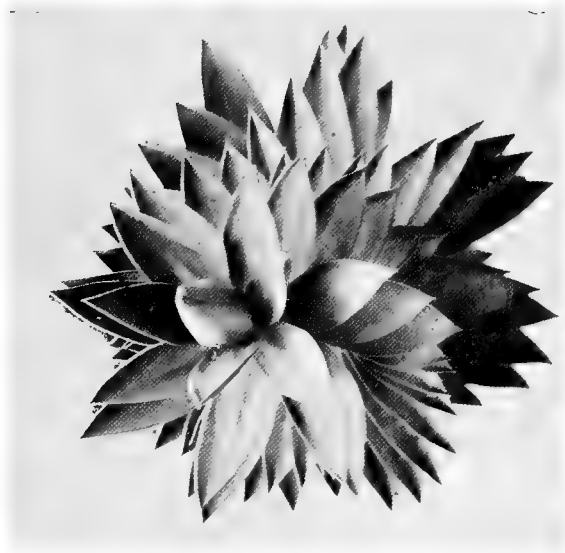
Fig. 77b.—The same shoot viewed end on.
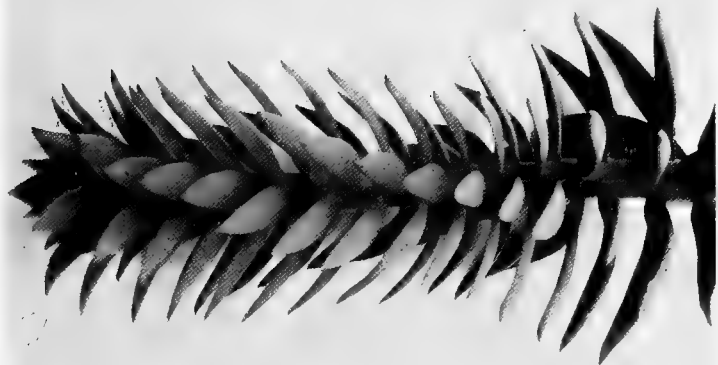
Fig. 77a.—*Euphorbia biglandulosa*, Desf. (3 + 4) shoot.=
7-spired.

an anomalous mode of forming the transitional 21 series in the capitulum itself is clear from the form $(29+47)$, fig. 54, in which the contact parastichies of the involucre are seen to be $(11+18)$, and the rise of phyllotaxis so far follows the normal course. The $(29+47)$ capitulum is again of special interest in that it does not represent the normal sequence of expansion from the $(3+4)$, which includes all the other anomalous heads.

III. *Low ratios of the anomalous series.*

Such constructions occur more commonly in plants which exhibit marked xerophytic specialisations, and are associated with normal spiral systems in closely allied species, but less generally with the whorled condition in the assimilating shoots. There is little reason for regarding them as *markedly beneficial* to the plant, although it is clear that the nearer the ratios approach equality the less exposure there will be in the long run to intense light, if the axis is condensed, although possibly no two leaves are mathematically superposed ; the assumption that they represent variations in the production of down-grade assimilating shoots appears more probable. They should thus be especially characteristic of the leafless Cactaceae and Euphorbiae, and such is in fact found to be the case. (*Cf.* special section.)

Thus the very beautifully seven-spired *Euphorbia biglandulosa* closely resembles in habit and glaucous foliage *E. myrsinites*, which possesses normal $(2+3)$ structure, and both form normal Cyathium inflorescence shoots. *E. myrsinites* varies from $(2+3)$ in weak axes to $(3+4)$ in the strongest : it is thus difficult to avoid the conclusion that $(3+4)$ represents a weakened form of $(3+5)$ (fig. 77).

Similar variations occur in succulent Saxifrages and Crassulaceae.

Sedum acre with normal $(3+5)$ foliage shoot passes into a whorled $(5+5)$ flower, symmetry being attained as usual beyond the calyx members.

Sedum reflexum with a $(3+4)$ or seven-spired shoot, produces terminal 8-merous flowers, while the lateral scorpioid cymes contain 6-merous flowers, the variation of the assimilating shoot being thus passed on to the reproductive shoot (figs 76a, b).

Sedum elegans, as previously noted, varies from $(5+8)$ to $(6+10)$.

Monanthes polyphylla forms rosettes of $(8+13)$ or $(7+11)$, the flowers being symmetrical and $6-8$-merous : 7-merous flowers are common also on $(7+11)$ shoots.

Such phenomena present a close parallel to the case of multijugate

types, and are evidently due to a change in the bulk-ratio of the
seedling, which may be rare in "normal plants," but becomes common
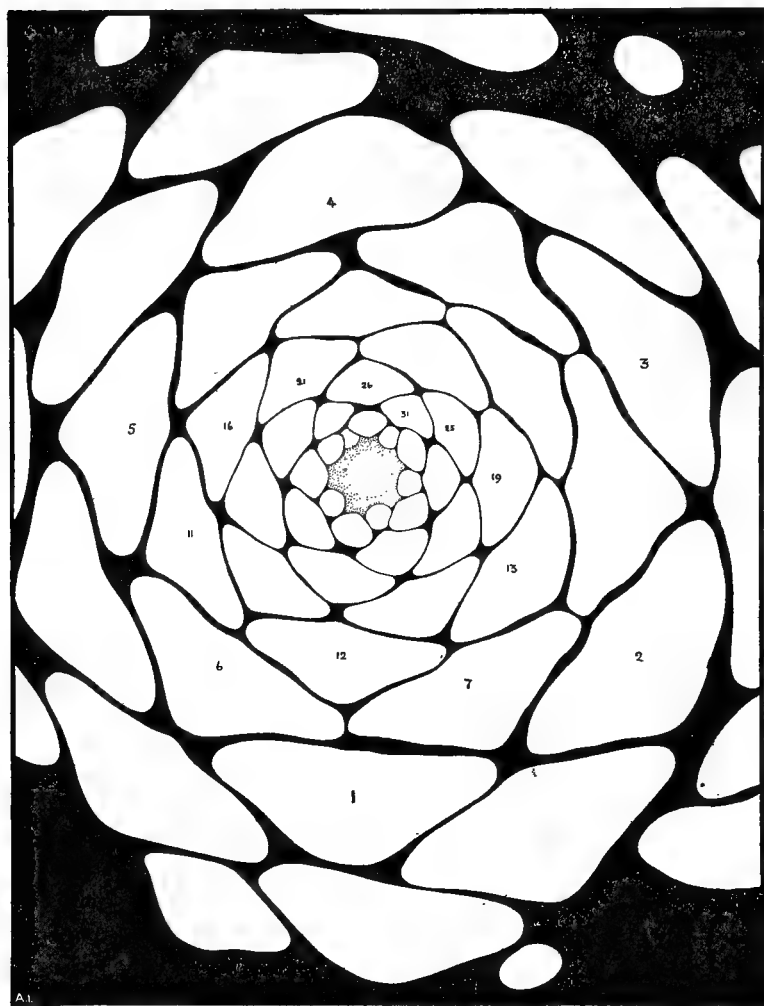
Fig. 78.—*Lycopodium Selago*, L.   Shoot-apex (5 + 6).

in plants showing marked xerophytic adaptations, and even a specific
constant in certain forms.   In such variations the " Fibonacci sense "
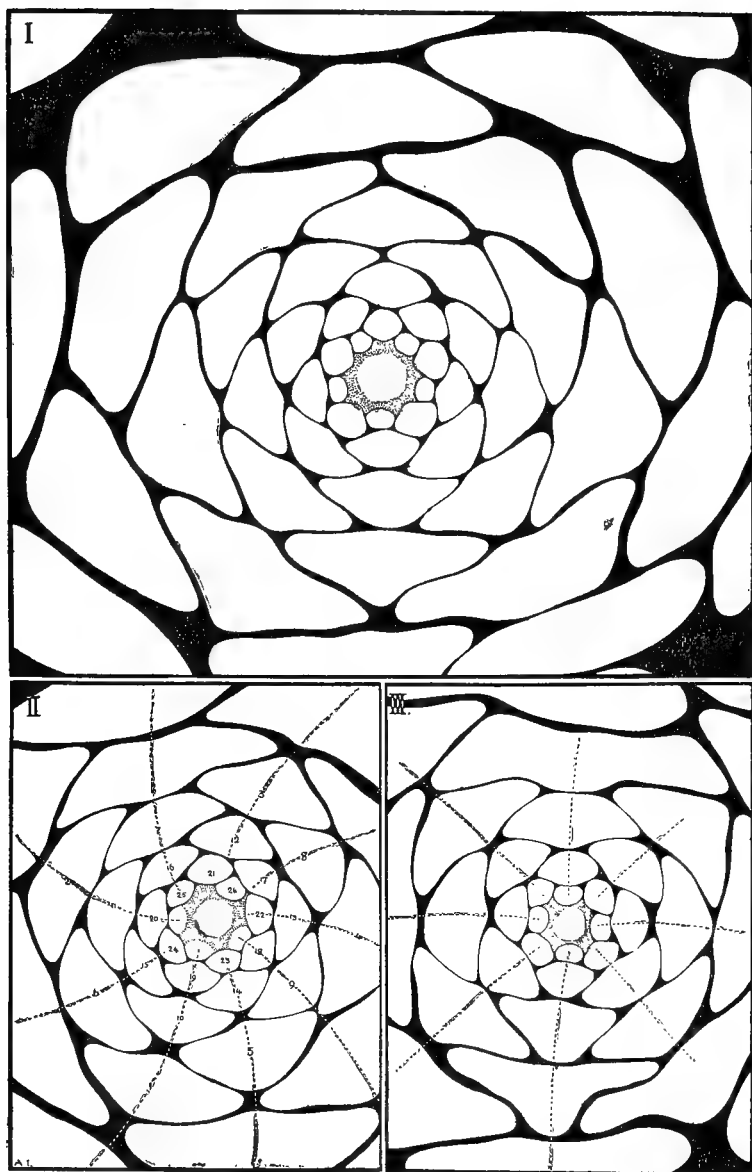
Fig. 79.—*Lycopodium Selago.* (5+5), (4+5), and (4+4), the two last being twin-shoots of a dichotomy.

may be again said to be lost, and the system may be explained as in *Araucaria* $(7+11)$, and the bijugate $(6+10)$ system, from the standpoint of a change in the bulk-ratio; but the question is only removed one degree farther on, seeing that the reason is now required as to why in such plants the bulk-ratio becomes modified.

One of the most beautiful examples of such variation is afforded by *Lycopodium Selago*. The leafy apices are easy to cut, the leaf members are all uniform and very little modified, and branching of the main axis takes place by dichotomy of the apex, and not by the reduced axillary shoots.

Parastichy systems are exhibited in the forms—

$(5+6)$, $(4+5)$, $(3+3)$,

$(5+5)$, $(4+4)$, $(2+2)$, (the last being found in the axillary shoots), and transitional stages may be observed.

Thus out of 20 apices, 7 were $(5+5)$,
 5 „ $(5+6)$,
 5 „ $(4+5)$,
 2 „ $(4+4)$,
 1 was $(3+3)$.

Comparison of a series of such apices, drawn under the same power, shows at once that the round leaf-primordia are constant throughout, but the diameter of the apex varies, and becomes gradually smaller in correlation with the lowering of the bulk-ratio (figs. 78, 79, 80).

The special point of interest, however, is the close approximation to symmetry, and the large proportion of symmetrical cases found. Thus 10 out of 20 apices were symmetrical, while the small lateral bulbils appear to be constantly $(2+2)$.

In such cases, where, as theoretical diagrams indicate, the primordia subtend an angle of between 50° and 60°, small changes in the bulk-ratio cannot explain the whole of the phenomena. As already shown, the bulk-ratio for $(4+4)$ is practically identical with that of $(3+5)$, and the bulk-ratio in such constructions cannot therefore be regarded as the sole determining factor; but behind these phenomena there appears a controlling power which is aiming at a

still greater approximation to adult symmetry than that afforded by the Fibonacci series.

Similarly a still closer approach to symmetry may be indicated by the assumption of such ratios as $(6+7)$, $(7+8)$, $(8+9)$, $(9+10)$, etc., and these are to be observed more especially among the *Cactaceae*, in which any biological effect implied in decreasing the leaf surface exposed to light is nil. (*Cf.* special section.)

IV. Once it is granted that a new row of members, implying the opening up of a new spiral path, may be initiated at any point on any expanding axis, or again dropped out on a decreasing one, without necessarily implying the corresponding change all round the system, it is obvious that a vast number of anomalous systems may be secondarily produced, as in the case of *Dipsacus* taken by the Bravais. Among the variety of ratios thus obtained, some, as soon as they happen to be divisible by a common factor, would be classed as multijugate; so that it now becomes clear that the *multijugate condition is only a special case of an anomalous construction*, and often no doubt produced by the same causes.

While, however, the multijugate primary condition has been regarded as a break in the direction of symmetry consequent on the loss of the Fibonacci series, it does not follow that such will always explain anomalous secondary systems. The very fact that new curves may be added singly, without compensation, throughout the rest of the system, shows that the sense of symmetry has deteriorated.

In dealing with any given case, therefore, it becomes of interest to see what alteration is made at any given change of system.

Does the change, that is to say, make for symmetry, or the reverse?

In other words, is a long curve added or a short? Similarly in reduction, the loss of a short curve makes for symmetry, as expressed by equality in the ratios; the loss of a long curve renders the construction more asymmetrical.

Remarkable examples are afforded among the Cactaceae, in which any alteration in the phyllotaxis system is rendered obvious by a corresponding addition or loss of a vertical ridge. The change will often be observed to make for *asymmetry*; the following examples suffice :—

1. *Melocactus communis*: semi-globular form, showing 21 ridges, formed by a system $(9+12)$; a new short curve added raised the system to $(9+13)=22$ ridges.

2. *Cereus chilensis*: specimen forming a cylindrical shaft 6 feet high, ridges at level of ground $14=(7+7)$. The axis was thus symmetrical and remained unchanged for a height of 5 feet, including about 1200 members. A new ridge was then put in, and the system raised to $(7+8)$, and this remained constant for about 75 members.

A second new ridge was then put in (fig. 39*b*), raising the total to 16, and this system was continued to the growing point.

It becomes, therefore, a point of interest to note whether the symmetrical condition of the greater portion of the shaft was regained, or whether the change was quite aimless.

The latter proved to be the case, the new parastichy system being $(7+9)$.

On the other hand, a variation which makes for *symmetry* is shown in *Lycopodium Selago* (fig. 79). Twin branches, one of which, as is frequently the case, develops more rapidly than the other, showed at their apices the systems $(4+5)$ and $(4+4)$, the former being about 1 mm. taller than the latter. The asymmetrical shoot thus shows 9 spiral series of leaves; the symmetrical one 8 theoretically vertical orthostichies. As a matter of fact, small growth movements connected with the assumption of dorsiventrality and unequal development render the lines drawn through the centres of construction slightly distorted (fig. 79, 2, 3).

On examination of these lines in the $(4+5)$ system, it will be seen that a break is commencing at the member numbered 12. Thus 21 falls too much on one side of 12, so that 26 is still more on one side of 17, and does not make contact with 22, its predecessor along the " 4 " line. The visible system is thus preparing for the intercalation of a new long path, which will raise the curves to $(5+5)$. In contrast, again, to the case mentioned of the symmetrical *Cereus chilensis*, a shoot of *L. Selago*, with the symmetrical construction $(3+3)$, was observed to change directly to $(4+4)$ (fig. 80), so that the symmetry was purposely retained.

V. Finally, just as accidental variation may give a bijugate system, or anomalous systems with very nearly equal ratios, so, as

soon as equality is reached, *the symmetrical construction follows as a mathematical consequence.* How small the change may be is shown, for example, by comparing the structural diagram for a $(6+7)$ with a $(6+6)$. The result, however, is very striking in that an accurately simultaneous formation of a whole cycle of members is substituted for a serial formation; but it serves to bring out the fact that the actual appearance of the members, in time, has possibly little to do with the mechanism which produces them within the protoplasmic mass of the apex. It is important to note that the
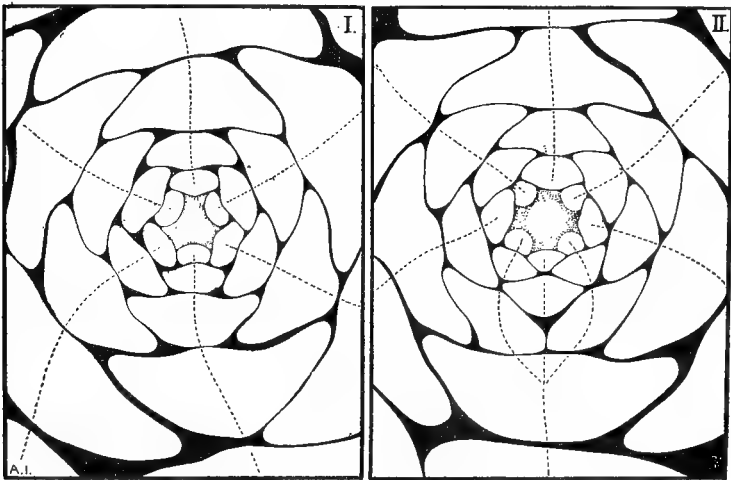
Fig. 80.—*Lycopodium Selago,* $(3+3)$ and $(3+3)$, changing to $(4+4)$.

simultaneous formation is a mathematical fact dependent on the manner in which the construction is directly changed from a presentation in terms of a spiral-vortex to that of a circular one.

In many Cactaceae, such an assumption of symmetry appears to be entirely accidental (*cf.* special section), and asymmetry may be again produced. In the case of specialised *decussate* assimilating shoots, the fact that reversion to asymmetry may take place in the sporophylls (*Calycanthus*) has been held to support the view that the decussate condition is of biological utility. An example, again taken from *Lycopodium Selago* (fig. 80), shows that symmetry is

retained, and new paths are added symmetrically (as in *Equisetum*) by the bifurcation of old ones, although the change of bulk-ratio which requires to be negotiated in adding two new curves is very considerable.

To sum up, anomalous ratios are rare in normal plants, but are especially characteristic of specialised inflorescences and xerophytic assimilating shoots of such plants as *Sedum, Euphorbia, Lycopodium, Cactaceae.*

So long as they are *primary constructions*, they imply a reduction of the Fibonacci sense; but with the loss of the Fibonacci ratios, there is correlated a general independent attempt at symmetry as expressed by equality of the ratios, with the general result that these are less than $(1 : 1.62)$; while in extreme cases the approximation is so close that the anomalous system may often be regarded as the exception.

They represent modifications of the normal phenomena of phyllotaxis, and occur as local, individual, or even specific variations. Taken in connection with multijugate systems, they may be regarded as a second case of a break towards adult symmetry, as opposed to a symmetrical building mechanism. The loss of the Fibonacci series is more complete, and the capacity for independent approximation to actual equality in the ratio is correspondingly increased.

Special interest attaches to the case of *Lycopodium Selago* in that here the "Fibonacci sense" appears to be entirely lost, and the approximation to a construction which involves a nearer aproach to adult symmetry is so close that strictly symmetrical examples are as general as the asymmetrical approximations. Viewed from the standpoint of a plan of building, it is clear that the hypothesis of an oscillation-angle can no longer explain the mechanism (*cf.* fig. 78), since the system is built on a distinct spiral path; and on the other hand, the view that the "genetic-spiral" is the determining factor, while it gives an interpretation of the asymmetrical cases, only exaggerates the gap which has been held to exist between asymmetrical and symmetrical constructions. That such constructions may be really separated by only very trivial distinctions appears to be shown by the occurrence of cases like that of the twin

shoots of a dichotomy, $(4+4)$ and $(4+5)$ (*cf.* fig. 79, 2, 3); and that this is not a rare or exceptional occurrence is shown by the fact that identical appearances may be found among the shoots of Cactaceae (*cf.* special section, *Echinopsis*).   The conclusion appears fully warranted, that these apices have impressed on them a set of curves, adjusted to the relative size of the lateral member required, which give an approximately symmetrical construction ; any accidental variation in the ratio which involves inequality necessarily produces an effect of spirals, while equality in the number of intersecting curves implies the subsequent appearance of whorls.*

Thus in dealing with anomalous constructions, the interpretation of the facts observed in terms of a genetic spiral is only possible when the system remains constant, and even in comparatively simple cases the enumeration of the parastichy ratios may prove to sytematists a simpler method of describing the facts observed.†

In all cases, in fact, except among the very simplest constructions, the " genetic-spiral " hypothesis becomes somewhat of an incubus ; it is quite useless, but still one does not like to throw it over completely.   It is true that all complicated constructions are more simply regarded as systems of intersecting curves, and that once such a system is in working order it appears to act along the curved paths of the parastichies, adding or losing these curves as required ; but in the simplest cases on which the spiral construction for asym-

---

* *Lycopodium Selago* presents a point of great interest in that the terminal growth-centre, which clearly is not expressed in terms of an apical cell on the broad flat apex, definitely bifurcates and two independent growth-centres result, each of which initiates its own curve system, with little regard to the other or to the parent centre.   These relations have been investigated by Cramer (*Pflanzenpys. Unters.*, Nägeli und Cramer, iii. p. 10), and not only may the shoots of the dichotomy give dissimilar systems, either symmetrical or asymmetrical, but in cases of both being asymmetrical the genetic spiral may work out either homodromous or antidromous, and thus in one case antidromous to the parent axis.   The suggestion is obvious, therefore, that all such new growth-centres produce their systems quite independently and adjust their own bulk-ratio and symmetrical relations.   The new systems may with difficulty be expressed as bifurcations of older paths, so far as these reach round each half ; but in terms of genetic spirals they become still more involved, in that, as already seen, true symmetry is readily attained.   (*Cf.* Cramer, Plate XXIX. figs. 9-13.)

† *Cf.* Schumann, *Monographia Cactacearum.*

metrical growth was founded, as in the case of the three-sided apical-cell of the Fern, the genetic spiral is present and apparently actually represents the asymmetrical formation of new growth-centres, one at a time. To what extent this can be regarded as holding for the more complicated production of the growth-centres of more massive primordia must necessarily be obscure, until more is known as to what is really implied by the convention "growth-centre," and how far such a centre has any material existence, or possesses a finite character.

It is meanwhile interesting to note that the genetic spiral as a single determining path was the creation of Schimper, and that the older writers, including Bonnet, were content with the expressions "Multiple Spirals," "Parallel Spires," for even slightly complicated constructions. The deduction of a single genetic spiral is, in fact, the result of the assumption of a spiral of Archimedes as the fundamental growth spiral. The utilisation of such a spiral, passing through equidistant points on the radii vectores, is clearly the simplest mode of expressing such a construction; and Sachs is so far correct in stating that the orthostichy system of Schimper and Braun is preferable to the parastichy system of the Bravais: if a given set of points can be defined in terms of two sets of spirals, but also in terms of one spiral and definitely straight lines, the latter is certainly preferable. But with the elimination of spirals of Archimedes straight lines vanish (for practical purposes), and the points of intersection of log. spirals can only be defined in terms of two of the orthogonally intersecting curves; the genetic spiral thus becomes useless theoretically, since its complementary orthogonal path is not obvious, while the parastichy ratios are simple and readily observed and tabulated. The genetic spiral thus tends to vanish as the log. spiral theory replaces that of Schimper and Braun, but at the same time the "orthostichy" curves are often so nearly straight that the Schimper-Braun formulæ will remain very useful in a large number of cases for descriptive purposes; nor can there be any objection to such a proceeding so long as the convention is recognised.

The error of the older phyllotaxis systems which postulate spirals of Archimedes is, however, more deeply seated than appears at first sight; it now becomes evident that its introduction into Botany

was due to an entire misapprehension of the phenomena of proto-
plasmic growth, as was only natural when protoplasm was still un-
known (1754–1835). By regarding growth as the addition of
layers of equal thickness in equal times, as in the conventional
representation of the addition of annual rings to a tree, expressed
in terms of concentric circles with equal increments on the radii,
a conception of *arithmetical progression* was introduced, which
naturally resulted in the adoption of the spiral of Archimedes.
A clearer recognition of the interstitial growth of a mass of proto-
plasm throughout its whole substance, by becoming expressed as a
series of concentric circles in *geometrical progression* which may
contain a network of similar figures, leads equally naturally to the
assumption of a log. spiral as the actual curve of asymmetrical
growth.

Finally, it must be pointed out that the whole of the observations
and deductions hitherto given for phyllotaxis constructions, in-
cluding systems expanding and falling according to the Fibonacci
law, *are the expression of the geometrical properties of intersecting
spiral curves, without necessarily adding any further information
with regard to the character of the spirals*; and almost any pair of
unequal curves will give approximate results. The appearance of
log. spirals will be produced subjectively by arranging any collection
of *similar figures* in spiral series; and it is thus necessary to keep
in mind Sachs' original observation that the subjective appearance
does not necessarily tell anything of the mode of formation of a
given construction. The log. spiral theory demands *orthogonal
intersection*, and this has so far not been proved, although it might
be legitimately hypothecated from the analogy of the orthogonal-
intersection theory of cell-formation proposed by Sachs; since it is
sufficiently clear that if the segmentation of the plant-body in
terms of cells and cell-layers can be expressed by orthogonal
trajectories, there must be some law behind these phenomena
which controls the distribution of growth-energy, and this may
prove to be in some way comparable to that which governs more
strictly physical phenomena.*

* "Sections through growing, and especially through young parts of the plant,
always show arrangements of the cells which are quite definite, and in the

The point therefore remains,—*How far is this appearance of orthogonally intersecting log. spirals possibly a secondary effect produced by building a system of approximately similar protuberances?*

This problem may be attacked by assuming the orthogonal log. spiral construction as expressing a distribution of growth energy and seeing whither it will lead—that is to say, by deducing the proper curves for the transverse component of the members, building the corresponding mathematical systems of what such phyllotaxis should be, and then comparing these constructions, and any deductions which may be made from them, with the familiar phenomena observed in a transverse section of a shoot-apex.

If the appearances agree, or can be made to agree within an intelligible range, when other secondary factors are allowed for, the orthogonal system may be regarded as proved for phyllotaxis, as one special case of a theory of growth distribution; and while proving this, the same deductions would further involve a confirmation of the original views of Sachs, which still remain somewhat hypothetical, in that they are based on appearances judged by the eye; and it at once becomes evident that this conception of the distribution of growth-energy in orthogonally-intersecting planes must be of the utmost importance in determining the primary space-form of the whole of the plant-body.

In thus dealing with phyllotaxis phenomena which present the appearance in transverse section of a system of intersecting curves, two points of view may be established. One, that of the builder, in which the addition of new elements in time is made the leading feature; the other, that of the architect, to whom the actual order of construction may be· immaterial. Is, that is to say, the space-form of a plant determined by the visible structure of the growing point—or is it an invisible property of the shoot, and the same growth form may be worked out in terms of different units? The

highest degree characteristic; the directions of the cell divisions are by no means accidental, and an observer sufficiently acquainted with geometrical and mechanical science at once recognises in the structures presented by the totality of cell-walls within an organ, cut in the proper manner, that we have here to do with a conformity to law, the true meaning of which, however, is difficult to decipher" (Sachs, *Physiology*, Engl. trans., p. 432).

presence of complicated growth forms in such plants as Fungi, Florideae, Siphoneae, and Lichens suggests what may be termed the architectural view, which Sachs has so greatly strengthened by his recognition of the fact that the apical-cell of Vascular Cryptogams, so far from being " the ruler of the whole growth in the growing-point," represents merely " a break in the constructive system." The more general standpoint has undoubtedly been that of watching the building processes, and this usually finds expression in the discussion of the fate of cell-segments.*

It is this possibility of drawing a distinction between the consideration of a given phyllotaxis system, as the product of one or more genetic spirals, or as a complex of intersecting contact-parastichies, which is so far the most valuable feature of the log. spiral theory ; in that, by regarding the same construction from two different standpoints, prejudice in favour of either one of them may be avoided.

* Sachs, *Physiology*, p. 433 : " It was formerly supposed to be possible to characterise the true morphological or phylogenetic nature of an organ by the way in which cell-division took place, and hundreds of treatises and laboriously drawn plates were devoted to the purpose."

ERRATA. (Part I.)

Page 6, line 31, *for* become   *read* becomes.
" 12, " 13, " interesting " intersecting.
" 23, " 10, " produced " produce.
" 34, " 12, " parobolas " parabolas.
" 39, " 17, " endodernal " endodermal.
" 69, " 26, " 1 : 1·5   , 1 : 2.
        (The omission of 1 : 2 affects all the ratios in
          the column.)
" 70, " 15, " inflorescence *read* inflorescences.

On the Relation of Phyllotaxis to Mechanical Laws.

By

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

Lecturer in Natural Science, Jesus College, Oxford.

PART III.

SECONDARY GROWTH PHENOMENA.

I. Notation.

In the preceding general survey of the phenomena of Phyllotaxis it has been observed that the arrangement of the lateral members (*appendages*) of the plant body of higher plant-forms exhibits remarkable phenomena of *Rhythm*, and the arrangement, that is to say, thus works out as a definite pattern. The exceptions to this generalisation are so few that these may be safely regarded as cases in which the rules have been complicated by further specialisation, or possibly by degeneration in the construction mechanism, and in the vast majority of cases the rhythmic character of the phenomena is their most distinguishing feature.

In so far as the phenomena are rhythmic, the observed facts admit of mathematical expression ; but at the outset it becomes extremely important to distinguish what exactly are the data afforded by the plant itself, and what conceptions may have been gratuitously introduced into the study of the subject. In the historical development of botanical science it was unavoidable that the first generalisations of plant-morphology should have been founded on the contemplation of adult plant structures, on shoots, for example, which possessed nodes and internodes : a

P

curiously academic view of a plant thus survives very generally in text-books which bears little reference to the facts of ontogeny and the manner in which a leafy shoot is actually constructed. The fact that all internodes are secondary and subsidiary growths, and that the elongation of a typical shoot is a secondary and extremely complicated phenomenon, is often forgotten or unexpressed. The fact that the arrangement of leaves on such shoots produces the subjective effect of circles or winding spirals is also entirely secondary, the primary construction system only being observed at the apex of the shoot, or on shoots which exhibit no secondary elongation whatever.

Leaving on one side, therefore, all academic prejudices in favour of *whorls* and a single *genetic-spiral* traced on an elongated leafy axis by drawing a subjective line through successive members, the actual data of the rhythm exhibited by the plant in building its leafy shoot system reduce merely to the enumeration of a certain number of curves which intersect in either direction. No further data can be obtained from the living organism than such observation of these intersecting curves, the *contact-parastichies*. These are therefore simple numerical expressions involving two whole numbers only ; and not only so, but every additional factor read into the subject comprises, to use Sachs' expression, "gratuitously introduced mathematics."

There can be, however, no objection to the introduction of the mathematical properties of the numbers, since the numbers are given ; and the fact that mathematics may be introduced follows directly from the presence of continued rhythmic phenomena. But error creeps in as soon as the bare numerical data afforded by the plant are combined to constitute a mathematical expression or formula. The facts of observation supply an intersecting system of equally distributed spiral curves, the number of which must be integral and can usually be readily checked. The only additional mathematical data that can be introduced, therefore, are the mathematical properties of such intersecting curves. But in expressing the relation of the numbers of these intersecting curves, care must be taken to render the resultant expression mathematically harmless. To this end, the notation has been

adopted of connecting the two numbers by the sign $+$, which may be taken as meaning simply *and*, or more pictorially as a *cross*.

The data are simply that so many curves cross so many, nothing is added as to the angle of intersection, and such a formula includes the simple facts of observation.

Any attempt to indicate a *ratio* introduces a source of error ; the formula (5 : 8) would mathematically imply a construction by log. spirals in that ratio ; and, although it has been suggested that such is actually the case at the growth-centre, the expression has been avoided until the proof appears more satisfactory. Still greater is the error of the old notation which states that 5 and 8 parastichies imply an $\frac{8}{13}$ genetic spiral with orthostichies as straight lines. Such a mathematical statement is alone possible for the spirals of Archimedes and helices originally postulated by Bonnet and Calandrini for adult constructions.

It has been pointed out that in no *growing system* is any helical construction possible, and that the retention of the old fractional notation constitutes a hopeless state of confusion which still vitiates much of the literature of the subject ; since it is clear that no theory which implies unstated the mathematics of helical construction, and which therefore deals with members of equal bulk or points equally spaced, can ever afford any insight into the construction of a growing system of gradated primordia. In no instance is the unfortunate error of this gratuitous interpolation of helical mathematics more conspicuous than in dealing with the phenomena of contact-pressures ; the two things cannot coexist in the plant. Contact-pressures must be growth-pressures, and equal volume is only attained in the lateral members at the close of their growth period, when growth-pressures cease with the growth of the members : when they are mutually pressing one another they are not equal in size, and the Archimedean notation becomes so misleading that deductions involving this standpoint are often quite unintelligible.[*]

While, again, the genetic-spiral hypothesis only includes a certain number of phyllotaxis constructions, all such rhythmic patterns may be considered from the standpoint of the simplest method of

[*] *Cf.* Schwendener, *Berichte Deutsch. Bot. Gesell.*, 1902, p. 264.

reading the pattern—that is, as a complex of intersecting spiral curves. The mathematical properties of such intersecting spirals are readily deduced mathematically, and still more obviously by simple geometrical constructions, of which several examples have been previously given (figs. 25, 26, 28, 55, 63, 70). From these it becomes clear that, in dealing with such intersecting curves, three cases are mathematically possible, and all occur widely distributed in the plant-kingdom.*

First, if the two integers which express the spiral curves in either direction are divisible by unity only, one spiral of the same class can be drawn through the entire series of intersections. A numerical value can be given to all the points of intersection by counting along the spirals in either direction numerals differing by the number of the same spirals in the set. The fact that such a numerical value can be given is a mathematical consequence of the peculiar curve construction ; and in this case, since one spiral passes through the entire series of points, the numerals utilised are successive numbers (Braun's method).

Secondly, if the two integers are divisible by a common factor (n), n spirals of the same class can be each drawn through $\frac{1}{n}$ of the points of intersection (fig. 70) ; the same method of numbering up does not utilise successive numerals, but gives n sets.

Lastly, as a special case of the preceding, equality of the integers results in the same number of spirals passing each through its own share of the points ; but each set of points lies on a common and readily observed circular path.

These three sets of mathematical phenomena are properties not of plants but of intersecting spiral curves. They follow in the plant because the rhythmic expression of phyllotaxis takes this particular form of distribution. Why it should take this form, is of course the next fundamental question. But so far it will be seen that the first case constitutes the condition of normal spiral phyllotaxis, extremely general because the Fibonacci ratios

* For the general proof of these statements in mathematical form I am indebted to Mr H. Hilton ; for log. spirals or spirals of Archimedes it can be shown geometrically on the diagrams.

commonly utilised agree with the rule. The second case is that of the multijugate system, while the most special third case is the familiar one of whorled arrangement in which successive whorls alternate.

All these phenomena, again, are more simply and correctly described in terms of the curve systems. It has been noted that only in the first case is there a single spiral which can be isolated as an *ontogenetic* spiral; and the fact that such a spiral can be isolated, and is consequently seen when the whole system undergoes a very general, though entirely secondary, elongation, is a geometrical accident of the construction, however useful such secondary elongation may be in the plant economy. The recognition of this spiral on adult plant-forms by Bonnet is thus necessarily responsible for the peculiar inverted manner of regarding phyllotaxis phenomena, and although the inverted mode of expression is common to many branches of plant-morphology, there is no justification for the continuation of such lines of thought at the present day.

II. Rhythm.

IN previous chapters a general theory of growth was enunciated, according to which the production of new members might be capable of mathematical expression and of geometrical representation in a diagrammatic form. That growth is distributed at the apex of a shoot in such a manner that its *transverse component* may be expressed by a plane circular construction around a central point (the *growth-centre*) is sufficiently clear, in that the circular section of the vast majority of plant axes is evidently the outcome of such a regular and symmetrical distribution from the "growing-point": so much so, in fact, that any stem which is not circular in section is generally recognised as the result of secondary inequalities in the rate of transverse growth. On the other hand, it is clear that such a generalisation is based on an unexpressed physical conception of radial growth; and although it is thus possible to imagine a stem which will be mathematically circular in section, it does not necessarily follow that such a stem ever occurs in nature; nor would it be expected, owing to the recognised frequency of secondary irregularities in every growth-system. The fact that no stem is mathematically circular in section does not affect this well-established generalisation; but it is necessary to point out that such ideas involve a physical conception which, as in other cases, must ever be the basis of any system of morphology.

Exceptional cases, apart from the production of angular and ridged stems, and the band-like forms produced by uneven secondary growth in thickness, may be included under three types:—

I. The *cladode* form, in which the shoot becomes secondarily
flattened in one plane, by a more rapid growth in that
direction than in any other (*cf. Opuntia*).

II. The *fasciated stem*, usually though not necessarily classed
as a monstrosity.

III. The so-called *dorsiventral shoot*, in which *centric* growth is
replaced by an *eccentric* distribution which involves the
phyllotaxis system.

In the first of these cases (*Opuntia*), section of the apex (fig. 81)
shows that the original phyllotaxis pattern is normal, and only
becomes distorted at a subsequent stage.

In the "fasciated" system, the centric distribution around a
point (the single growth-centre) is changed for an attempt at
similar distribution around a number of such centres (*cf.* monstrous
flowers of Buttercups with two or three distinct gynoecial cones,
and double Daffodils) or around a longer or shorter series of such
points constituting a line, with the result that great disturbances
ensue, owing to the impossibility of normal uniform growth ex-
pansion in such a system ; the resultant paths of which would,
along the flanks of the crested apex, be represented by parallel
straight lines replacing the intersecting curves, which would still
appear at the ends of the system. These appearances are well
shown in the case of a fasciated shoot of *Oenothera* (fig. 82) ; the
whole of the curved crested apex, over an inch in length, could
not be cut in one transverse plane, but a small portion suffices to
show the marked irregularities produced both in shape and series
of the foliage-leaves as their growth expansion brings them into
new and anomalous contacts.

The case of the change from centric distribution to eccentric,
the so-called *dorsiventral* shoot, may be left for subsequent dis-
cussion ; it is only necessary so far to point out that the con-
struction lines of its phyllotaxis system should continue to be
represented by orthogonal trajectory curves, just as those of the
eccentric starch-grain apparently follow the same laws as those
presented by centric forms.

In such a circular growth diagram, again, the result of a uniform
rate of growth in the whole system may be expressed by a

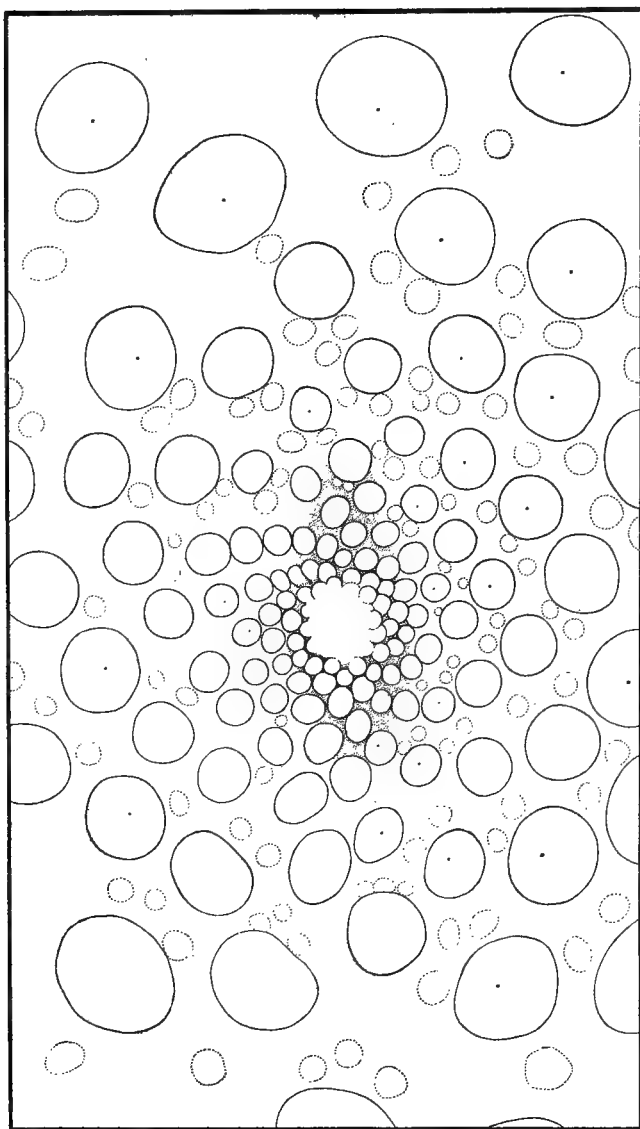Fig. 81.—*Opuntia leucotricha*, P. DC. Apex of spring-shoot, system (8 + 13), rendered bilateral by secondary cladode formation (sections of the spines dotted): cam. lucid.

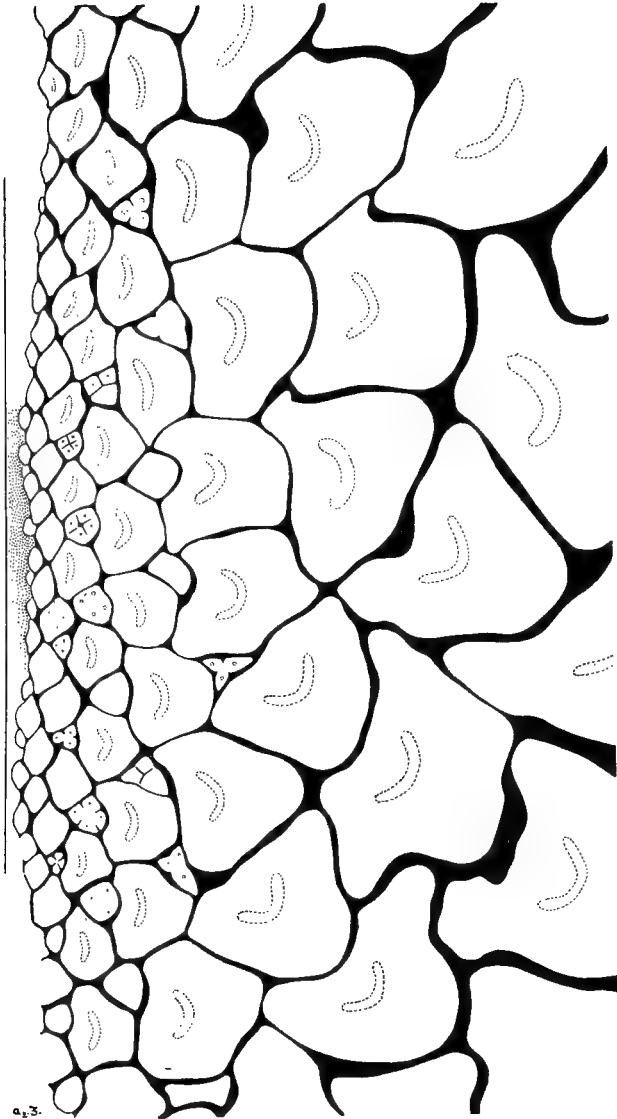Fig. 82.—*Oenothera* sp.   Apex of fasciated shoot (perennating rosette) ; portion of
section $\frac{1}{10}$th the whole length and 4 mm. long : cam. lucid. drawing showing
irregular expansion curves ; axillary flower-buds tetramerous and trimerous.

circular meshwork of quasi-squares, in which all the similar meshes are produced in equal times—it being evident, as previously pointed out, that the consideration of an ideal condition of uniform growth should precede any attempt at a closer approximation to the facts of growth actually presented by living organisms. While, again, this geometrical presentation of uniform growth is so far simple in its radially symmetrical relations, a geometrical device admits of homologous cases of asymmetrical growth also being plotted, thus giving, as already described, a figure identical with the geometrical representation of lines of equal pressure and paths of flow in a spiral vortex.

In such a system the introduction of *lateral* growth-centres may be next considered. That such a secondary growth-centre should repeat the construction of the primary centre appears fully warranted as a sound hypothesis. The phenomenon of a lateral growth-centre is thus to be similarly planned by a circular meshwork of quasi-squares, and the figure illustrates similar relations expressed in terms of equal time-units. It may thus be taken that a lateral growth-centre may be similarly represented either by a true circle, or possibly by the homologue of a circle : the two cases may be subsequently distinguished.

In the arrangement of such lateral members, again, one of two conditions must obtain : either the system is wholly irregular, or it is regular and systematic. The former case is apparently presented in certain specialised inflorescences (*Ficus*) and floral axes (*Clematis*), androecium (*Paeonia, Cereus*), but not in positions in which it can present any claim to be regarded as representative of a phylogenetically primitive arrangement; and when the construction is thus irregular, little can be said about it beyond the fact that the impulses apparently obey no law which can be formulated, other than the statement that they appear to be very approximately equidistant.

On the other hand, in the vast majority of plants, especially in unmodified vegetative shoots, as previously pointed out, the regularity of phyllotaxis formations is their most remarkable and distinctive feature; and this clearly implies at least an equal

regularity in the initiation of the impulses which produce new centres of lateral growth.

Thus it follows from observation of plant systems that such lateral growth-centres producing a sequence of similar foliage members are always similar figures at similar ages, and that these are so arranged that they make similar contacts with adjacent members. In other words, if the lateral growth-centres are represented as circles, they must be arranged in some manner after such schemes as shown in figs. 19, 20, 22, 23, so long as the simple case of uniform growth is postulated. That is to say, in that the lateral members are similar figures they will fall along lines plotted by equiangular spirals, intermediate between the limiting cases of the straight line and the circle; and in that they may be represented by "circles" in lateral contact which would be contained in the quasi-squares, the contact lines of such series must necessarily be orthogonally intersecting equiangular spirals. The log. spiral theory of phyllotaxis is thus the necessary outcome of :—

I. The theory of the geometrical representation of a uniform growth-movement.

II. The hypothesis that a lateral growth-centre is essentially of the same nature as the symmetrical growth-centre originally postulated.*

* It has been stated above that the lateral growth-centres would be expressed as true circles or as the homologues of circles inscribed in the meshes of the square meshwork. That the latter is probably the case in the formation of leaf-members is very clear from the fact that circles cannot be placed in the accurate contact relations required ; this being especially noticed in low systems which in the plant are apparently as regular in formation as higher ones.

A simple and fundamental conception of a *leaf* as opposed to a branch is thus brought out, which constitutes, in fact, a true mathematical distinction between an *axis* and an *appendage*. A *leaf* is a primary appendage belonging to a system controlled by a central growth-centre, a subsidiary development of it, differing from it in its increased rate of growth, and is thus represented by the quasi-circle homologue, the controlling growth-centre remaining at the apex of the shoot. A *branch* or lateral axis, on the other hand, is represented by a true circle, that is to say, as a new growth-centre wholly uncontrolled by the growth-centre of the parent shoot, and maintaining its own

Although uniform growth may be postulated for the main shoot, or at any rate in some part, however small, of the First Zone of Growth in which the new impulses are being initiated, it is clear that if growth proceeds at the same rate from the lateral growth-centres as well, these will never make any relative progress nor produce any visible result, although they may have been mapped out in the construction system. Nor is a rate of growth in the lateral members at first slower than that of the parent axis conceivable, since the insertion of the lateral members constitutes the surface of the axis itself. In botanical phraseology, therefore, so long as the rate of growth in the primordium and axis is equal, the lateral growth-centres remain "dormant." No visible effect, then, can be produced by growth from a lateral growth-centre unless its rate of growth be greater than that of the system as a whole. In such case the expansive development of each lateral centre will be continued until contact is established with adjacent members. Thus, in the simplest conception of a growing system of stem and leaves, uniform growth may be postulated for the main shoot, and uniform growth, but at an increased rate, for all the lateral members, the result being that the growth of the lateral member becomes visible as a disturbance of the original equable system, and protuberances are formed which come sooner or later into close lateral contact.

Observation of the plant shows that such methods of arrangement actually prevail, and the regularity of the construction, especially as indicated by the contact-lines, is its most fundamental and important feature. Nor again is it possible that any such regularity can ever be a secondary effect; comparison of systems in which primordia are less regularly formed, and exert unequally distributed contact-pressures on one another, as in the case of the growth of fasciated shoots, and in the apparently centrifugally

growth-centre at its apex as a perfectly independent system. This view further suggests that the imperfectly individualised growth-centre which gives rise to a leaf outgrowth *remains at the point of its insertion,* and the apparent presence of an apical cell in certain leaves would thus appear to have nothing to do with their space-form, but is, as in the case of the shoot itself, only a part of the mechanism by means of which the architectural form is worked out.

developed androecium derived from a circular zone of growth (*Paeonia, Cereus*), shows that such secondary influences will only increase the primary irregularity.

Since, as hypothecated, the geometrical construction of a circular meshwork of quasi-squares indicates a *time-diagram,* that is to say, one expressed in terms of rate of growth, and the above constructions follow the lines of such a diagram or its asymmetrical homologues, it is clear that the system must be first interpreted in terms of *time,* and that the regularity of the system is the expression of a remarkably beautiful *periodicity* or rhythm in member production.

That regular phyllotaxis phenomena are really the expression of such accurate periodicity in member production will be readily granted; but such a statement does not take one very far, since it is only another way of expressing an obvious fact. The point is, —to what is this periodicity due, and will it afford any further insight into the phenomena? Thus, once such periodicity is granted, it is clear that the phenomena of "rising" and "falling" phyllotaxis may be very elegantly expressed from this standpoint, in that a rising phyllotaxis and high ratios would imply an increased activity of production of new growth-centres on a given area, correlated with an increased vigour in the axis; while falling phyllotaxis and low ratios become a sign of enfeebled growth— that is to say, growth-centres are only produced at greater intervals of time, with the result that they each influence a wider tract, and thus give rise to members of relatively greater bulk, so that the system presents the subjective appearance of a smaller number of intersecting curves. But, on the other hand, it affords little further insight into the causes affecting other phenomena of symmetry, bijugate systems, etc. Thus, in dealing with symmetrical as opposed to asymmetrical systems, periodicity can go no further than the expression of the simple fact that in the former case several members are simultaneously produced at equal intervals of time, while in the latter case only single members are produced at equal intervals.

There must, in fact, be some still more hidden meaning in the construction, from which the periodicity as expressed in a time-

diagram, and in actual ontogeny, follows as naturally as does the geometrical construction by logarithmic spirals from the addition of similar members.

The perfect regularity of the system shows that it is not the ultimate shape or the lateral contact of the members which is the essential controlling feature; the form may vary with subsequent growth changes, and the similarity of the contact-relations is again only the expression of regular periodicity of formation. Whatever subsequent changes take place, the primary curves drawn through the centres of construction of the lateral members, in the great majority of cases, retain their numerical relations, the only difference being in the form of the curves themselves. Still more remarkable is the fact that in many cases even the secondary lateral axes subtended by these primary members (*Helianthus*), or emergences based on them (Pine-cone), maintain the original curve system with such constancy that phyllotaxis theories are discussed from the standpoint of these structures, which have only a secondary relation to the true lateral members.*

The essential point to note is that in order to produce such a degree of regularity the actual centres of lateral growth must have been initiated at definitely established points; that is to say, an infinite number of causes might produce secondary irregularities once a system were laid down: the fact that any system can be traced in the adult condition implies that the initial impulses must have been not only equally regularly placed, but presumably far more so.

Thus, in the postulated construction of circular growth-centres plotted along orthogonally intersecting log. spirals, the numbers of which are taken from observation of the plant, it follows that these initial centres must also have been laid down at the intersection of orthogonally intersecting log. spirals of the same ratio. The main question at issue, therefore, is to determine why these points should be found at the intersection of certain orthogonal

* *Cf.* Jost, *Bot. Zeitung*, 1902, p. 21, "Die Theorie der Verschiebung seitlicher organe durch ihren gegenseitigen Druck"; Leisering, *Flora*, 1902, p. 378, "Die Verschiebungen an Helianthusköpfen in Verlaufe ihrer Entwickelung vom Aufblühen bis zur Reife."

trajectory paths, and what may such paths and intersections possibly mean from a physical standpoint—that is to say, to what extent may the diagrams be also taken as the expression of a field of distribution of growth-energy, comparable, for example, to manifestations of distribution of the physical energy of the electro-magnetic field ?

To what extent one may be justified in thus passing from a *kinematic* to a *kinetic* standpoint is, of course, very questionable; and similarly little can be said beyond mere speculation until more is known as to what is actually meant by the expression *growth-energy,* or the energy of life, and how far it is comparable, for example, with " electrical " energy. One point may, however, be conceded : that in the case of living matter, *the actual mechanical energy accompanying life obeys physical laws just as surely as its material substance obeys chemical laws.*

The data afforded by the plant are these :—

    I. A growing, expanding system, containing, therefore, moving particles ; in which

   II. Growth-energy is being introduced from a central " growing-point " ; and

  III. A construction which, as expressed in the transverse component of the formation of lateral members, has been put forward as implying primarily the geometrical properties of orthogonal trajectories.

How far, then, can analogues be found for such a system in the domain of physics ; and how far is it possible to press such an analogy, as indicating some fundamental law of protoplasmic growth ?

Further, in the discussion of symmetrical and asymmetrical phyllotaxis (*cf.* Part II.), it became increasingly evident that, while the hypothesis of a single controlling ontogenetic spiral gives no satisfactory clue to the general phenomena of all varieties of phyllotaxis, all such systems might be readily interpreted and discussed in terms of series of intersecting curves—the contact-parastichies. These curves should, therefore, have some meaning attached to them. If, as the log. spiral theory suggests, these curves imply lines of equal distribution of growth-energy, it may

be possible to give an explanation in physical terms; but, on the other hand, it is clear that, if the intersections are never orthogonal, the data given by the plant are so obscure that the phenomena of phyllotaxis only become the more hopeless of explanation. So strongly is this standpoint suggested, that it appears well worth while to assume the consequences of orthogonal intersection and base all hypotheses on them; since, if the view is a mistaken one, the error must become apparent sooner or later; while, so long as no such error appears, it may be assumed that the hypothesis of energy-distribution is a workable one.

The use of the word *action* in previous chapters (*cf.* Part I. p. 36), as a generalised expression, has been since avoided, as in its strict mathematical sense the term undoubtedly places the subject in too complex a light to be at present available for botanical purposes: its introduction was mainly based on the necessity for indicating that the systems presented phenomena of movement, without reference to any obviously unattainable data as to the actual velocity of any units which might be regarded as component particles. Since the actual velocities of the particles of a growing plant-apex are extremely small, a closer analogy may perhaps be found, so far as the present purpose is concerned, in a two-dimensional electrostatic magnetic field whose properties may be considered as depending on each quasi-square portion of space, enclosed by lines of force and equipotential lines, possessing the same amount of potential energy. Just, in fact, as in the above case the same amount of potential energy may be considered to be situated in each quasi-square, so in the plant-apex the same amount of growth-energy, *i.e.* that required for the production of a single leaf-primordium, is localised in a single quasi-square of the phyllotaxis diagram.* Or, on the other hand, if growth-energy be considered as more analogous to kinetic energy

---

* A botanist would probably be more inclined to state the converse proposition: the fact that an equal amount of energy is presumably directed into each lateral primordium, granted a constant relation between axis and primordium, would involve such a geometrical construction. Either way of looking at it is sufficient for present purposes.

than potential energy, a similar distribution of energy will be found in the two-dimensional motion of an incompressible fluid.*

But it must always be borne in mind that such hypotheses of equal energy-distribution only deal with the hypothetical region included under the conventional expression "growth-centre." Away from this region, which represents a more or less gratuitous conception, and which, being beyond the range of actual observation, must also always remain hypothetical, retardation of growth ensues, and tends to produce rapid deformation of the log. spiral systems. Similarly, in the case of eccentric growth, deformation immediately sets in at different rates on different sides. Hence any theory of energy-distribution involving equal amounts of energy on every square must still remain hypothetical, though the quasi-square system, whether deformed by retarded or unequal growth-rates, will continue to indicate *equivalent growth-areas*; and such areas mapped by the intersecting curves, whatever the

* Again, even the homology of vortex construction is open to objection, since, although it was expressly stated (Part I. p. 36) that the terminology of spiral and circular vortices was introduced as a *metaphor* to make clear what was implied by a certain type of geometrical construction, the idea of a spiral vortex appears to carry with it an impression of *spiral movement*.

It cannot be too strongly insisted that *no spiral growth-movement either exists in the plant or is implied by the log. spiral theory.*

The theory may be a spiral one, the phyllotaxis may be justly termed spiral, since the pattern seen may be expressed as spirals, *but the growth-movement is absolutely radial.* (*Cf.* Weisse, *Prings. Jahrb.*, 1904, p. 419.)

It is in this sense that the suggestion of Sachs is so valuable and correct, that "all the spirals are subjective"; and as a purely psychical phenomenon it is interesting to note how the spiral pattern of a moving mass insensibly leads many observers on to the interpretation of a spiral motion (*cf.* Goëthe) just as phyllotaxis has been for a similar reason inundated with *torsion theories.*

It is, in fact, one of the best points of the log. spiral theory here put forward that not only is the *growth-movement* regarded *as radial*, but it can be shown mathematically that even in a centric spiral system such lateral primordia are bilaterally symmetrical about the radius along which they travel away from the growing-point. (*Cf. Mathematical Notes*, Form of the Ovoid Curve.)

Further, in order to avoid the repetition of a "spiral" standpoint, the expression *asymmetrical* is definitely adopted as a better mathematical mode of expression.

Q

subsequent mathematical form of these may be, will exhibit the results of equal growth in equal times.

Two points may be here conceded : there must be, as already stated, some mechanical law implying a fundamental property of force and matter underlying these phenomena of rhythm; and it will again be hardly possible to discuss such speculations without trespassing on the terminology of some branch of physical science, the fundamental laws of which are really equally obscure. Thus, choice has been suggested between the terminology of the electro-static field, vortex-motion, or even the crystallisation * which constituted the basis of Nägeli's micellar theory. There is no suggestion that phyllotaxis has anything to do with any of these physical phenomena; but certain features capable of geometrical presentation by orthogonal trajectories, common to these physical phenomena, appear also to result from the determining causes of phyllotaxis. The essential point at present is,—granted the geometrical theory can be established for phyllotaxis, what inferences can be drawn from it from a physical standpoint, any or none ? When physicists are in a position to state that the conceptions by means of which they are led to the mathematical laws of phenomena are necessarily absolutely correct, it may be possible to further discuss what ultimate bearing the similar orthogonal construction may have in the case of living protoplasm. Till then it is at any rate remarkable that such similarity should be found, and few will doubt that, as Sachs pointed out for cell-structure, some law evidently controls the whole series of phenomena, which must again be a fundamental property of living matter. If the introduction of a mathematical conception of growth and growth-centres can lead to any better method of dealing with the facts, there will be no harm in trying to apply

---

* The general facts of crystallisation are even more remarkable in that they refer to inanimate matter. Thus it may be possible to deduce mathematically the number of crystalline forms, but the prime cause which determines why crystallisation should ever take place, or why some forms should be commoner than others, or why a given substance should select a special form, is as remote as any indication of the prime cause of phyllotaxis. The number of arrange-ments possible in phyllotaxis is relatively small, and the observation and tabulation of their occurrence comparatively simple.

it, so long as "growth-movement" and "growth-energy" are re-cognised as being in some way comparable, though not necessarily identical, with more strictly physical phenomena. While, again, the application of the strictly mathematical conception of a uniform distribution of growth-energy around an initial growth-centre must remain necessarily in the condition of a working hypothesis, since it can only apply to a region which is itself somewhat hypothetical, in which the rate of growth is conceivably uniform, *there can be no doubt that such an hypothesis must continue to form the basis of all considerations of the geometrical representation of the growth-phenomena presented by the plant-body;* and before passing on to the discussion of the numerous conditions which may be superimposed on such an elementary phyllotaxis system, it may perhaps be as well to sum up the points which so far appear definitely established.

Thus, in Part I. (*Construction by Orthogonal Trajectories*), it appeared increasingly evident that the general method of accumulating phyllotaxis data by the observation of orthostichies was hopeless, not only from the standpoint of actual observation, but a consideration of the mathematical propositions of Schimper and Braun showed that helical constructions had become applied to something they were never intended for, *i.e.* to the developing systems at the growing-points, in which, since the spirals are obviously neither helices nor spirals of Archimedes, the postulated helical mathematics no longer held, and the systems of orthostichies as vertical lines vanish for theoretical reasons, as also for practical purposes. The study of *orthostichies* thus became eliminated from phyllotaxis, while the value of *parastichies* and the *genetic-*spiral remained unassailed.

In Part II. (*Asymmetry and Symmetry*), on the other hand, a general consideration of the phenomena of the phyllotaxis systems most commonly exhibited in the plant-kingdom clearly brought out the fact already noted in the preceding chapter, that mathematical systems of intersecting curves presented different phenomena, with the result that the *genetic-spiral* only held for one out of three possible cases, and this again only so long as the system remained constant. Since the *genetic-spiral* conven-

tion only applies to one special case, and does not hold for the *whorled* and *multijugate* systems, it is clear that the so-called genetic-spiral also vanishes from theoretical considerations; since now it is seen to be merely a property of a special arrangement of intersecting spirals, it can tell no more as to the meaning of the phenomena then was previously known. The creation of Schimper, it retains a certain interest as a relic of the past, but can now only be regarded as a *convention* which is often useful in practice owing to the fact that it admits of a method of attributing a numerical value to the members which, so long as growth is distributed equally around the growth-centre (*i.e. centric*), is actually a *time-sequence*, and expresses the order of ontogeny as checked by observation. It must, however, be remembered that this sequence, obtained by resolving a certain number of inter-secting curves along a single path, will necessarily cease to be a time-sequence if once the growth-system becomes *eccentric* (*cf. Eccentricity*).

With *orthostichies* and the *genetic-spiral* both eliminated from the subject, the *parastichies* alone remain, not only as the data to be accumulated by observation of the plant, but as the ex-pression of the working mechanism of the construction. Using again what must be perfectly metaphorical language, since borrowed from strictly physical conceptions, the log. spiral theory suggests that new centres of lateral growth are originated at the points of intersection of curves, which may be regarded as indi-cating a type of segmentation of the protoplasmic mass, wholly independent of cell-formation, along paths of distribution of equal growth-potential which may be so far homologised with " Lines of Force." To bring these curves into homology with equipotential lines it is required to prove that the intersec-tions are primarily orthogonal. The method adopted consists in assuming the fact, and continuing subsequent mathematical deductions with a view to render the error of the theory apparent. So long as no marked discrepancy appears, the theory may be regarded as a fair approach to the description of the conditions actually prevailing in the field of a " growth-centre."

The log. spiral theory again clearly differs fundamentally from all conceptions of "induction" in that the initiation of the new centres which work out the pattern remains wholly within the control of the construction centre at the apex of the main shoot, the living protoplasm of which would thus appear to possess a certain power of numerical choice. In other words, the paths of the construction forces are *centrifugal*, and not, as the induction theory would suggest, *centripetal*.

III. Contact-Pressures.

THE existence and great importance of contact-pressures has been emphasised by Schwendener, as also the fact that the contact-lines follow those of what has previously been described as a " concentration-system." It has also been seen that such growth-pressures may be referred to an increased rate of expansion in the lateral primordium as compared with that of the parent axis. This increased rate of growth implies that growth initiated from a new growth-centre extends radially and equally in all directions until contact is made with adjacent centres of growth distribution ; and in the great majority of cases it would appear that the visible rise of a primordium has some relation to the formation of contact surfaces ; although in other cases (*cf. Aspidium*, fig. 35) there can be no doubt that the primordia rise from a central region before any lateral contacts are effected.

It is clear that the existence of such undoubted cases of the complete absence of any lateral contact whatever, combined with the production of perfectly normal Fibonacci phyllotaxis, completely puts out of court all theories of phyllotaxis which demand the close lateral contact of primordia as being of fundamental importance in determining the initiation of new growth-centres, which has been such a favourite standpoint from the time of Hofmeister to that of Schwendener and his pupils. The construction of such an apex as that of *Aspidium* (fig. 35) is alone sufficient to disprove any contact theory, whether it be taken in the original form of mechanical contact-action, or in the diluted and still more hypothetical form of contact-stimulus. The essential point, how-

ever, is the determination of the ultimate value of contact-pressures when these do obtain.

From the general hypothesis of a uniform rate of growth in centric systems, it follows that all contact-pressures may be resolved into components acting along the orthogonally intersecting construction lines of the system; and so long as growth is uniform, *no displacement can ensue*, the only result being a change of form; the lateral members being, in fact, squeezed into the shape of quasi-squares. That contact-pressures may exist between growing primordia is undoubted, and that contacts are made in a "concentration-system": these are facts of observation. But it does not follow that they are in any way pre-eminently important in producing any displacements whatever in the developing system.

All theories of the effect of contact-pressures imply that the primordia just formed by the growing apex exert an *influence*, whether of the nature of a direct mechanical pressure or an "induction" (Weisse), on the centre which gave them birth. That such secondary centres of admittedly limited growth should thus impress their individuality on the parent centre of unlimited growth activities and control its subsequent operations appears at first sight somewhat preposterous; but this view has appealed to many botanists, and however much such a standpoint may be regarded with suspicion, since it represents an ideal *post hoc ergo propter hoc* type of argument, the essential point is to see how such a conception may have been treated from a physical or mechanical standpoint, and further, what may be deduced from it. It is clear to begin with that the amount of a contact-pressure cannot be estimated by the eye alone, and yet observations of effects which may or may not be due to such pressures constitute the only means of tracing such a theory. How shallow such interpretations may be is well seen, for example, in a criticism of Winkler by Weisse * in which a three-angled apex is said to be clearly due to the pressure exerted on it by three leaves which have been just produced from it, and are naturally moving away from it with the continued expansion of the growing-point. Nor

* *Prings. Jahrb.*, 1903, p. 413.

can there ever be much use in such observations unless the amount of pressure can be put into the mathematical theory. The so-called mechanical theory is thus not mechanical in any sense; it is based on pressures which cannot be measured, or even proved to exist, and may therefore be wholly imaginary, and such theories are as useless as any other standpoint to which the stigma of " Nature Philosophy " may be attached.*

In considering the special standpoint taken up by Schwendener, and the importance attributed by him to displacements, it must be remembered that Schwendener formulated the Dachstuhl theory to explain the well-known observation that the general facts of phyllotaxis phenomena as seen in growing shoots did not agree with the postulated accurate angular divergences of the Bonnet-Schimper helical system : and also that the most important piece of obvious evidence of such alteration was afforded by the very general displacement of the angles of primordia which become angular under mutual pressure. This latter feature may be considered separately ; at present it is only essential to point out that displacement of angles does not necessarily imply displacement of the whole member, and that, the Schimper-Braun Archimedean formulæ having been shown to be fundamentally incorrect for developing systems,—the error of the construction being rendered clear by the log. spiral theory,—the correction of such constructions by hypothetical secondary displacement becomes wholly unnecessary.

Schwendener's theory, put forward in 1875, has long held the field, since from the complexity of its assumptions its application to the plant was not easy to understand and still more difficult to disprove. The conception of what has been termed " bulk-ratio " was introduced as a factor in determining phenomena of spiral phyllotaxis ; but as previously shown, however valuable such a *convention* may be, it affords no clue whatever to the still more fundamental phenomena of asymmetry and the true symmetry of whorled construction (*cf.* Part II.).

Schwendener also assumed as facts of observation certain displacements of the lateral members, and close lateral contact

* *Cf.* Weisse, *Pringsheim's Jahrb.*, vol. xxxix. p. 419.

between the developing primordia: the fact that the Schimper-Braun formula did not hold for developing systems was common knowledge, but his method of connection of these factors into causal relation was extremely vague, and it may be noted that it never appealed to the critical acumen of Sachs (*cf.* also Pfeffer, *Physiology*, Eng. trans., vol. ii. p. 144). It may also be pointed out that, whatever importance be attributed to Schwendener's conception of the alteration of primary systems by hypothetical pressures, whether intrinsic, of the members themselves, or extrinsic, of some compressing agency, they have after all little to do with the fundamental facts of phyllotaxis, which is only concerned with the production of the primary system itself, all secondary alterations being subsidiary phenomena. Schwendener, in fact, still requires to prove :—

    I. The existence of any force producing displacement ;

    II. The fact that true displacements really are produced ;

    III. That such displacements are the result of the postulated force,

whether, again, the force be regarded as a mechanical agency or a still vaguer phenomenon of stimulation. The second of these points has been attacked by Schumann and Jost,* their object being to establish the fact, always sufficiently obvious to the unprejudiced mind, that such extensive displacements do not take place, and that the initial curve-system, as it first becomes visible at the plant-apex, persists in the adult condition unless rendered ambiguous by secondary elongation of the shoot.

The standpoint here taken up is not so much that Schwendener's theory is impossible,—it is founded on certain definite premises from which mathematical results ensue,—but that it is entirely gratuitous and unnecessary, since the phenomena it was intended to explain, *i.e.* the secondary alterations of the Schimper-Braun constructions, are non-existent ; while the premises themselves more than include all the data from which the log. spiral theory is mathematically derived—the very data, in fact, for which in previous pages stricter evidence has been demanded.

* L. Jost, *Bot. Zeit.*, 1902, p. 21 ; B. Leisering, *Flora*, 1902, p. 378 ; *Prings. Jahrb.*, 1902, p. 421.

As Schwendener's standpoint is somewhat involved and subject to modification, the following example of his original method may serve to illustrate the difference between the two conceptions. A well-known figure from Schwendener's first plate has been copied by Weisse into Goebel's *Organography*, and appears in the English translation (p. 75). A phyllotaxis system is supposed to be represented by (1) a set of spheres—a legitimate hypothesis, but still purely a hypothesis, since there is no evidence to show that the transverse section of a primordium is ever mathematically circular. (2) The spheres are taken as being all the same size: a condition which is never reached in the plant until growth has uniformly ceased, and the pressures with it. (3) They are arranged according to a helical divergence system of Schimper and Braun, which is all right once equal spheres have been postulated. (4) It is assumed that such an arrangement will give orthogonal loose packing; and finally, (5) an outside vertical force, an entirely hypothetical conception so far as the plant is concerned, is applied, with the natural result that the system may be ultimately thrown into close hexagonal packing. It is difficult to see what exact bearing such a conception, involving so many doubtful assumptions, can have on the arrangement of the gradated primordia arising on a radially symmetrical plant-apex; but, by taking the vertical force as a tension instead of a compressing force, it becomes clear that such a construction might approximately represent the changes produced in an adult system by passing it through the second zone of elongation, and which have been previously regarded as wholly outside the province of phyllotaxis, except in so far as it may concern the descriptive writer. In discussing Schwendener's standpoint, the first thing which requires to be clearly defined is the exact significance of what is to be included under the term phyllotaxis; is it to include all secondary changes in the system which may appeal to the eye, or has it to do solely with the actual forces which produce the primary system within the protoplasmic mass of the apex, without any reference to the details of cell-construction? Thus all phenomena of packing must be secondary: primordia must have been made and have reached a certain bulk before they can be packed. The agencies which

determine the initiation of new growth-centres are perfectly distinct from those which come into operation once they are formed and have produced members of a definite visible bulk.

The weakness of Schwendener's argument is sufficiently clear— the mere assumption of a cylindrical surface which may be unrolled at once puts all developmental phenomena out of court : the apex of a plant can never be regarded as a cylinder, although on the other hand it may never be quite flat; the unrolled cylinder representing, in fact, the longitudinal component of the growth-system which is solely due to a retardation in the rate of growth in a system which would remain always plane so long as uniform growth persisted. Similarly, the primordia can never be represented during development as equal spheres, nor possibly as truly circular in section. The assumption of circular figures, which will also be similar, and the orthogonal arrangement is alone all that is required to mathematically deduce the log. spiral theory ; since, when transferred to a plane projection of a growing-point, *no other spirals except log. spirals drawn in the manner previously postulated will continue to give either similar figures or orthogonal intersections.**

As already pointed out, the attempt to eliminate inconvenient spiral curves by unrolling the helix of Bonnet on to a plane is the point at which the initial error crept in. The helix represents the secondary stage of phyllotaxis, in which the members have attained constant volume by a progressive cessation of growth. A growing system is necessarily a log. spiral system or a derivative of one, and the helix drawn on a cylinder is mathematically related to both the spiral of Archimedes and the log. spiral of a plane projection, and may, therefore, be derived from either. Two of the five hypotheses of Schwendener, therefore, when applied to the transverse component of a phyllotaxis system, are sufficient to give the log. spiral theory, which agrees so closely with observed facts that no external agency, whether of contact-pressures, contact-stimulation, or anything else, is required to make the system

---

* I am indebted to Mr H. Hilton for the mathematical proof of these statements.

more in accord with a mathematical conception of what the relations of lateral members to one another should be.

As previously noted, the orthogonal quality of the system, and the possibility of representing primordia as either circles or the homologues of circles, the two points assumed by Schwendener, before postulating the disturbing agency, are just the two factors for which a more rigid proof has been sought. It will thus be seen that Schwendener's Dachstuhl theory can only apply to the displacement of members after they have been formed, and such apparent displacements are, no doubt, very general; they may be due to secondary bilaterality of the members, inequalities in the rates of growth of different parts of the members, as well as to different growth-relations between primordia and the axis. But all these features are secondary, and require to be carefully separated from the mode of initiation of the new impulses which produce the growth-centres of new members before these become visible.

Such secondary relations of displacement, so far as they may be due to contact-pressures, may be briefly considered from the standpoints of:—

    I. The pressure of older members on younger ones as they are formed.

    II. The reciprocal pressures of growing primordia against all with which they come into contact.

    III. The effect of a rigid boundary on a growing system.

So many entirely diverse phenomena have been included under the heading Phyllotaxis, that some consideration of these secondary relations of phyllotaxis systems is required in order to clear the ground before the primary and essential features can be treated without prejudice. To repeat the present standpoint,—Phyllotaxis has to deal with the processes which determine the rhythmic origin and regular arrangement of the *primary* lateral members (appendages) of a plant-shoot in the first Zone of Growth; the arrangement of primary members and secondary derivatives (lateral axes) on the adult stem being merely the relic of such a formation, which may have no obvious relation to the primary system. The fact that secondary axillary shoots, or formations of

the type of the Pine-cone scales, really do give a system apparently identical with the true phyllotaxis relations of the primary members, affords a curious witness of the deep-seated faith of observers in the laws of uniform growth ; and thus the Composite capitulum, the Aroid spadix, and the Pine-cone have always been favourite examples of theories with which they have after all only a secondary connection (Schwendener, Jost, Leisering).

I. The Pressure of Older Members on Progressively Younger Ones.

Hofmeister first put forward the view that the presence of older members must affect the position of new ones ; and that new members in the vast majority of cases arise ontogenetically in close contact with older ones is sufficiently obvious ; it remained, however, for Schwendener to make such close contact the basis of a definite mechanical theory. But the value of contact-pressure theories is greatly discounted if examples can be adduced in which the primordia do not arise in contact at all, and yet present the normal appearances of spiral phyllotaxis (Schumann). Thus, in many large shoots with broad flat apices such is apparently the case (*Nymphaea*, *Sempervivum*, fig. 83) ; the latter may be taken as a type of these constructions. The youngest visible primordia are low elevations which show no boundary-line along the shallow depressions between them ; but so long as the primordia show any inclination to rhomboidal shape, a certain amount of contact must be admitted, and contraction in the spirit-material allowed for. In a broad apex such contraction may be greater in the longitudinal direction, and in this and other cases frequently has the effect of pulling down the growing-point into a slight depression. The only evidence that can be accepted of complete absence of lateral contact will be the retention by the primordia of their original approximately circular outline. Such primordia occur noticeably in the apices of species of *Opuntia*, where the leaves, though rudimentary, are better developed than in most Cactaceae (*O. cylindrica*, *O. leucotricha*); but most remarkably and easiest of observation in such Ferns as the common *Aspidium Filix-Mas*.
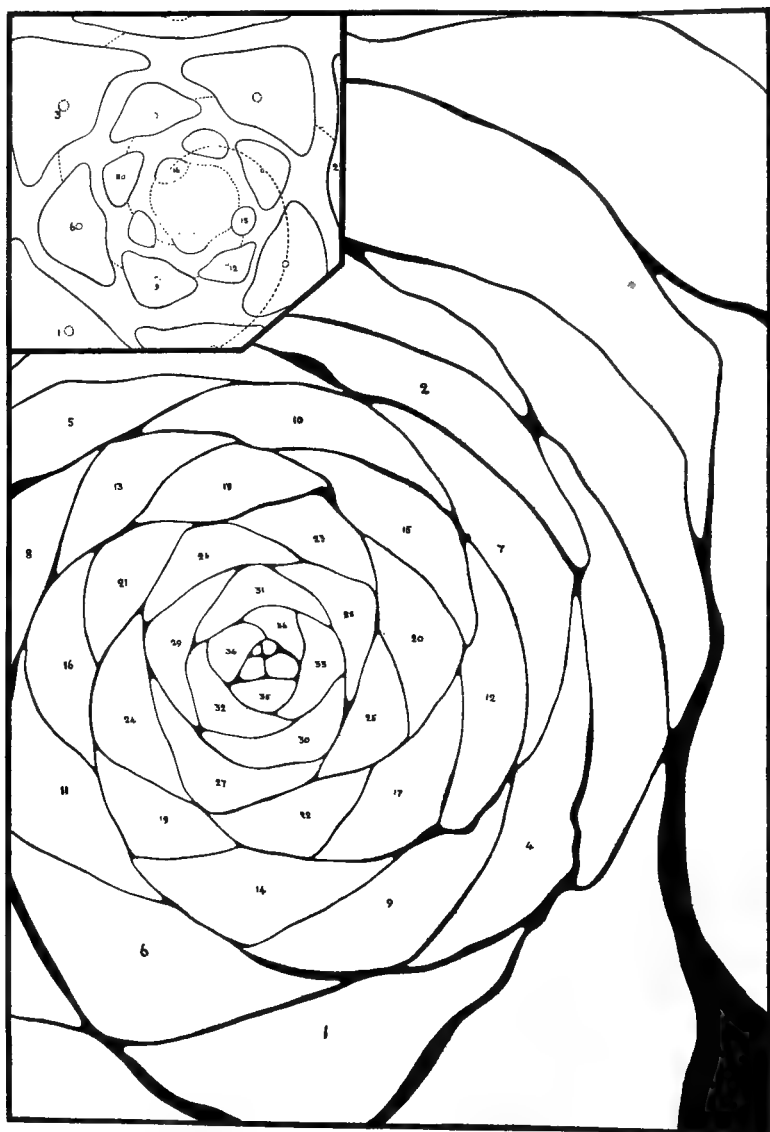
Fig. 83.—*Sempervivum tectorum*, L. Perennating rosette of adult plant cut above the apex, and the members numbered, showing secondary system (5 + 8); the smaller figure being the actual apex, showing system (3 + 5).

Perennating rhizomes taken from January to March show, within the coiled leaves of the current year, the primordia of the next season just commencing. On removing the chaffy scales, these appear as papillae, some quite visible to the naked eye, and also quite isolated from one another : Hofmeister's empirical generalisation, that each new member falls asymmetrically in the widest gap between two older ones, is as patent as in any small bud that requires to be sectioned. The system is made clearer by removing the entire apex, about ½ mm. thick, and rendering it transparent in Eau de Javelle (fig. 35).

Although destitute of lateral contact-pressures, the primordia arise each in normal position for $(3+5)$ or $(5+8)$ systems, and the lines drawn through empirical centres of construction form spirals, which intersect in the central region very approximately at right angles, so far as can be judged by the eye : the fact that this is the true structural condition being checked by examination of the stellar meshwork in the adult part of the shoot.

Again, consideration of the cell-structure of the apex of *Aspidium* root (fig. 18) shows clearly the general law of pressure as affecting younger members. Any younger cell can always grow successfully against all the pressures of older ones of the same character, and the apical cell grows against the pressure of the entire mass, and retains its walls always convex outwards. Similarly, any younger member can always compress an older one, and is therefore not essentially affected by it. In transverse sections of free leaf-producing buds, the primordia are again always convex outwards, and the preceding members become flattened : an example is afforded by *Araucaria* (fig. 41); new lateral buds flatten their subtending leaves, which would otherwise have remained rhomboidal in section. In more typical plants the older leaves themselves tend to assume a flattened appearance owing to their progressive bilaterality, so that the effect seen may not be due to one cause alone. In fact, when it is borne in mind that in a typical foliage-bud the axis which includes the leaf-insertions is growing and expanding simultaneously with the young primordia arising from it, it is clear that the subject of *bud-pressures* requires very careful handling, since when the whole system is growing uniformly there may be absolutely no pressures in the bud at all, the conventional expression " packing in the bud " being largely

due to a subjective impression which has no real basis. The very existence of bud-pressures requires to be proved in any given case.

The influence of the *pressure* of older members of the same system on younger ones may therefore be completely disregarded ; nor have visible primordia any directive influence on other primordia as they become visible : the relations of adjacent members being established, before the protuberances appear, in the actual substance of the protoplasmic mass.

II. RECIPROCAL PRESSURES IN OLDER MEMBERS.

Such pressures, as already seen, can only be due to an increased rate of growth in the primordia as compared with that of the axis, or to different rates of growth in different directions, or in different parts of the members. If, as by hypothesis, the members are primarily arranged in orthogonal series (loose-packing), all mutual pressure may be resolved into components along the orthogonal paths of the system : these, if equally distributed, can have no effect on the packing of the members, but if at all marked the *shape* will be altered, and the " circles " will become " squares." Only when the pressures are unequally distributed will any sliding effect be noticed, culminating possibly in close-packing of the hexagonal type. So long as growth is uniform, and the mathematical construction holds, the disturbing effect will be *nil* ; change of shape may take place, but no change of position.

In a great many leafy shoots this obtains to a considerable degree, and the leaf-primordia assume a rhomboidal form, as seen in transverse section, approaching that of a " square" of the log. spiral meshwork ; and this holds so long as growth proceeds uniformly throughout the whole shoot. The *fundamental section-form* of all leaves developed in closely packed systems is therefore that of a quasi-square with more or less rounded angles, the median line of orientation passing along one diagonal. Beautiful examples of such undifferentiated members persist especially among some Coniferae, in which bilaterality is small or wanting, and the leaf elongates to a " needle " type (*Cedrus atlanticus, Araucaria excelsa* ; *cf.* also *Mamillaria* and the Pine-cone).

On the other hand, evidence that growth ceases to be uniform is seen in the majority of leafy shoots. The quasi-square rhombs become flattened, the system is no longer orthogonal, a peculiar " sliding-growth " usually takes place, and the spirals tend to pass into spirals of Archimedes as the members attain equal volume and are spaced at equal intervals. Such cessation of uniform growth is produced by a lowering of the rate of growth in the lateral members; and such reduction, if equal in all directions, will tend to loosen the members from their close contact, and the bud " opens out." As the rate of growth is thus lowered in the primordia, contact-pressures necessarily vanish (*cf. Opuntia*). A special case is, however, general among leafy shoots : the rate of growth diminishes more rapidly in the radial direction than in the tangential, while in the latter the rate of growth may be apparently relatively increased. The same effect would be produced if the radial growth of the axis be diminished at a greater rate than the tangential growth of the leaf, owing to an apparent contraction of the whole system. These phenomena constitute the special case of the *bilaterality* of the so-called dorsiventral leaf, and may be considered separately. It is so far clear, however, that the effect of an increased tangential growth, real or apparent, must induce sliding of the members over one another ; but it does not follow that an internal thrust on the part of the members themselves can ever convert the system into any approximation to the hexagonal packing of the " pile of shot " type.*

* That is to say, if an orthogonal system of vertical and horizontal rows of bodies, free to roll over each other, be acted on by an external horizontal force, the horizontal rows are retained, but the vertical ones are displaced so as to intersect the horizontal at 60°. In the circular system of a transverse section, the vertical rows are represented by radii, and the horizontal by the circular paths : in the corresponding asymmetrical case, the vertical rows may therefore be represented by the shorter curves, the horizontal by the longer ones. The general result of any lateral thrust on the part of the members themselves will be that the shorter contact-curves become broken ; and this again is the phenomenon usually observed as soon as the primordia become markedly bilateral ; while the longer curves are retained unaffected, and are thus rendered increasingly conspicuous. On the other hand, a vertical compressing force (Schwendener), acting along the shorter curves therefore, would have produced similar flattening appearances, but would have tended to maintain

R

No evidence exists for the formulation of any theory of phyllotaxis to explain the origin of a normal asymmetrical system which involves the conception of the application of some *external pressure*. That the application of an external pressure on an empirically constructed system will produce results somewhat analogous to those seen in the plant, can never be an acceptable argument. While the action of an *internal pressure* set up by the members themselves may, it is true, subsequently alter the appearance of the system, but it can have no relation to the mode of its formation.

III. The Influence of a Rigid Boundary.

A boundary more or less resistant may be formed by older members of a character *dissimilar* to that of the uniform system previously considered. It has been previously pointed out that the youngest cells of a plant tissue will grow against practically any pressure that may be brought to bear on them in the living plant, and the same should hold good for the youngest members. This constitutes, in fact, the conception of *youth*. But such vitality is not necessarily long continued; this power of resistance usually rapidly diminishes. There is thus always a point at which cells or primordia begin to yield to surrounding pressures, and both cells and primordia as they grow older begin to assume the form adapted for least resistance to surrounding more rigid bodies, and fill the space available to them.

Such diminution of vitality is the more rapid in members which attain no great specialisation; or, more correctly, the

the vertical or shorter paths and have broken the approximately horizontal ones. Further, it must be noted that a cylindrical system of spheres arranged orthogonally would not pack by any pressure into a perfect hexagonally arranged one, in the sense of the accurate packing of the "pile of shot." The original contact-lines would necessarily be broken somewhere, and the resultant contact-curves would not present the regular arrangement which, on the other hand, as normally obtains in the adult plant as it does in the developing system. Nor, again, was there ever any reason to suppose that the whole leaf-primordia would slide over each other to such an extent when their bases constitute the surface of the axis.

converse should be stated—it is the diminution of vitality which renders them degenerate. This tendency to yield to outside pressure becomes, in fact, a measure of the decadence of growth-vitality and constitutes the phenomenon of "packing." Packing thus takes place in the case of both cells and lateral primordia as they attain their adult condition ; and the phenomena observed in the packing of cells composing ordinary parenchymatous tissue may be taken as a type of what is to be expected in the analogous case of lateral members. All growing-points lay down cells conceivably endowed at first with equal growth-energy, and arranged in layers the main periclinal and anticlinal construction lines of which, as Sachs pointed out, are probably orthogonal trajectory curves. As the rapid maturation of the specialised peripheral layers involves a reduction in their capacity for maintaining the rate of growth of the cells composing the inner tissues, and these latter tend to round off in order to produce the necessary intercellular spaces, the system falls into the irregular arrangement, approximating hexagonal packing, familiar in tranverse sections of a typical stem or root. Further pressures, especially well seen in the case of thickened members exhibiting sliding-growth, produce cell-forms often very approximately hexagonal in section.

Results somewhat similar should therefore be obtained in the case of lateral primordia which develop within a closed space and show feeble growth specialisations. To further satisfy the conditions, an apex is required in which the primordia are produced in a system with a fairly high ratio of curves, and a simple example is afforded by the winter-bud of *Cedrus*.

In *Cedrus Libani*, as in many other Conifers, the advanced xerophytic specialisation of the perennating foliage-buds takes the form of the protection of the young primordia of the foliage-leaves by means of a ring-growth of the stem which constitutes a well-marked cup, identical, in fact, with the circular zone of growth which in floral shoots represents the first stage in the development of perigynous and epigynous floral structures. Such a ring-growth may be conveniently termed the *crater* type of apex, as opposed to the normal production of a *cone* apex. In *Cedrus Libani* the crater is well marked, and, following the mechanical law of growth for such a lateral structure,

the more it develops, the more it tends to close over the apex, and hence exerts all the greater pressure on the enclosed primordia, the normal curve-systems for which should be (5+8) in small shoots. Longitudinal sections of such a bud (December) show the well-marked crater, the external surface and rim clothed with protective scale-
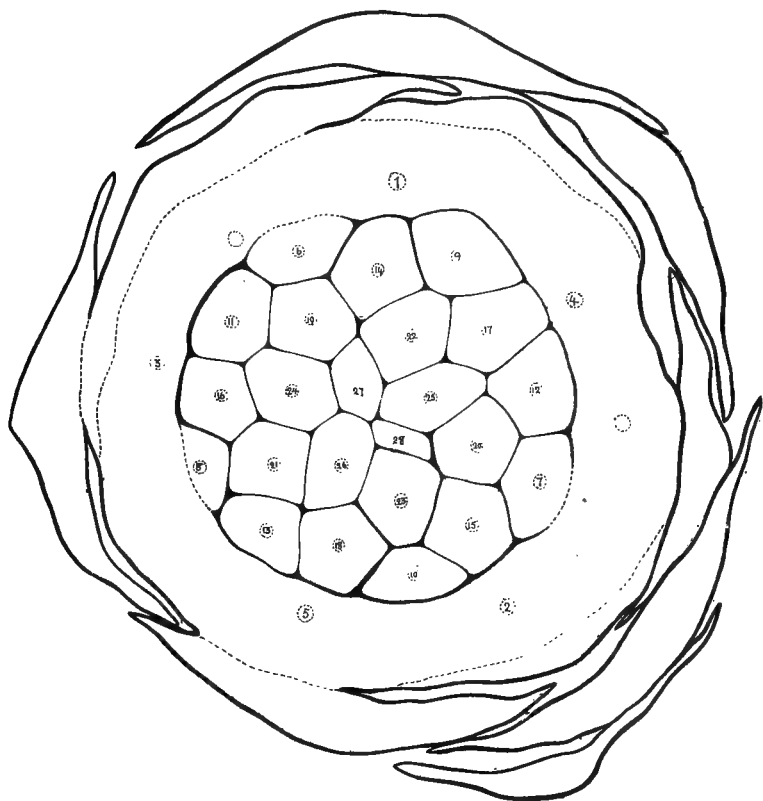
Fig. 84.—*Cedrus Libani.* Transverse section of winter bud, system (5 + 8), showing effect of pressure of crateriform axis.

leaves, the base of the inner surface producing the young foliage-leaves of the next season, and a conical growing-point rising from the base (fig. 85).

A transverse section just above the apical cone, passing through the crater wall, will show sections of leaf-primordia about three cycles deep (fig. 84). The nature of the packing is obvious, irregular hexagonal figures being produced, as in the packing of parenchymatous tissue;

PLATE XXVI.

Fig. 85.—*Cedrus Libani.* Longitudinal section of perennating foliage-bud, showing crateriform apex.
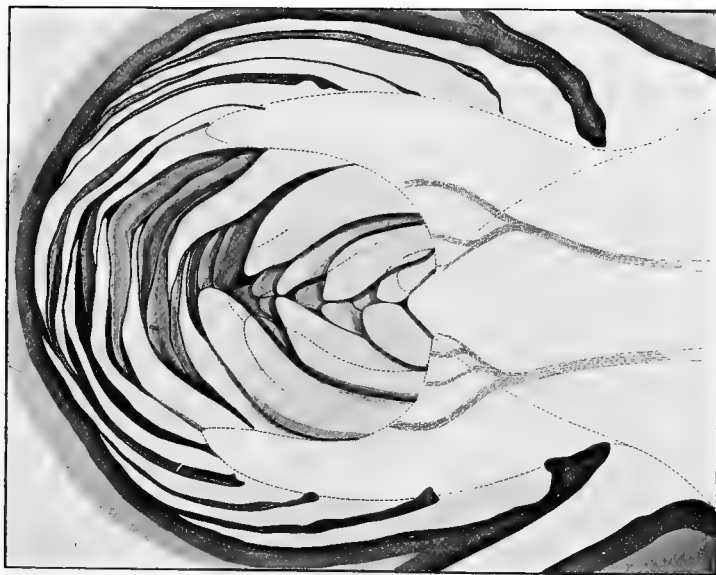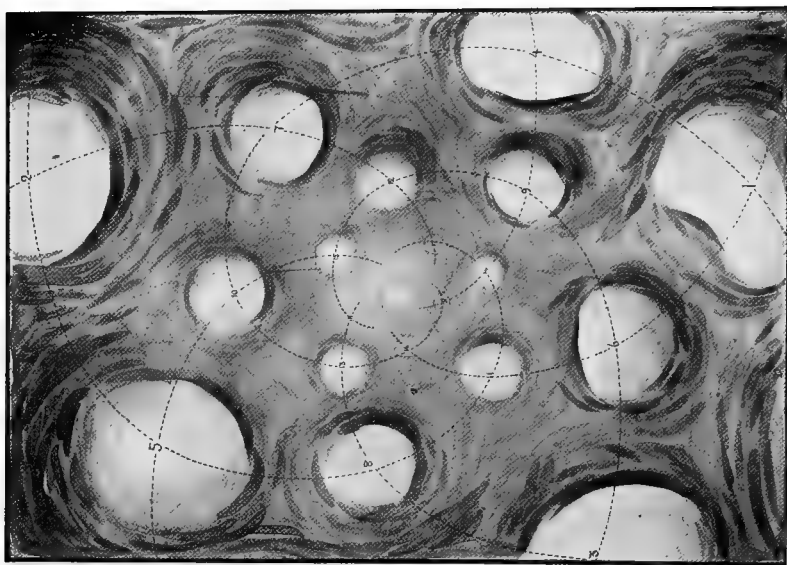

Fig. 35.—*Aspidium Filix-Mas,* growing-point (3 + 5).

and at first sight the $(5+8)$ system has been quite destroyed; but comparison of lines drawn through the central bundles of the leaves shows that it may still be traced with sufficient accuracy to admit of numbering the members.

The *Cedrus* bud thus represents a case of simple radial compression of the older leaves of a $(5+8)$ system against a circular boundary, the result being merely to produce irregular and often hexagonal figures; that is to say, owing to the effect of radial pressure the plastic masses of the older leaves are squeezed into irregular shapes, but they do not roll over one another to any extent. The phenomenon is rather one of adjustment of growth than of actual displacement, the centres of construction indicated by the vascular bundles remaining very fairly in their places. In dealing with such packing of leaf-primordia no analogy can be drawn corresponding to that of the packing of spheres into the hexagonal arrangement of the "pile of shot." The action of a radial compressing force, here provided by the overarching of the crater wall on the developing system, does not tend to produce displacements in any way comparable to those of the original Dachstuhl theory; the only result of such additional radial compression being the production of irregular figures resembling those seen on cutting a piece of ordinary parenchymatous tissue: the system tends to become irregular, but it is quite clear that no radial (*i.e.* vertical) compressing force acting on such a circular asymmetrical system would ever so change it that the system would after displacement retain a regular construction. The fact that in the general case phyllotaxis systems normally retain regular parastichy curves is therefore the proof that no extra pressures beyond those of the growing primordia are normally in operation.

Similarly, pressure against the relatively greatly developed cotyledons to a certain extent affects the shape of the first small needle-leaves of the seedlings of Conifers (*Pinus*, *Cedrus*). That such seedlings possess, so far as can be seen, an irregular phyllotaxis system may be due to more than one cause: that the actual curve constructions are at first anomalous and even sometimes symmetrical may be traced from sections which show the

curve-system of the vascular bundles supplying them, as they pass down the axis. Further, there can be no doubt that any production of an "expansion system" will give the appearance of irregularity, when the number of members developed before the change takes place is not sufficient to give the appearance of definite parastichies.

Thus *Pinus sylvestris* * commences very commonly with an approximation to a $(2+3)$ system, although the older shoots show $(5+8)$; and *P. Pinea* after initial irregularity settles down to $(5+8)$. In such specialised seedlings, as in the case of species of *Helianthus*, for some reason, the phyllotaxis is irregular at first, though this is by no means the general case for all plants. But the effect of pressure against the cotyledons so long as the plumule is enclosed between their bases, and these again by the endosperm, is well seen in the case of the first leaves which are initiated while the seedling is wholly within the endosperm and testa. Sections of such seedlings show very marked irregular packing shapes produced by pressure, much as in the bud of *Cedrus Libani*. Such pressures add, therefore, to the complexity of the determination of the systems as they appear at any given time ; but they clearly have nothing to do with the origination of the first impulses which determined the formation of the leaf-members in the substance of the broad embryo apex (fig. 86).

Comparison of the broad apex of a seedling in which the radicle has alone protruded (fig. 86, I.), with that of older seedlings, suggests most strongly that primordia are already being formed within it, but have not yet arisen above the surface. The space between the bases of the cotyledons is usually somewhat elliptical, and the primordia at the ends of the ellipse are distinctly more advanced than the others, so that here, as in other cases in which true centric growth does not obtain, the actual ontogenetic order of appearance gives no clue to the order of formation. There is as yet no regular system observable, since the number of leaves already in sight is insufficient to show contact-parastichies : the arrangement thus appears somewhat irregular, and, owing to the conical shape of the apex, is not readily observed in transverse section. Slightly older seedlings, in which the cotyledons

---

* *Cf.* Schwendener, *Bot. Mittheilungen*, i. p. 89, Taf. v. The number of leaves seen in section being too small to give any reliable pattern.
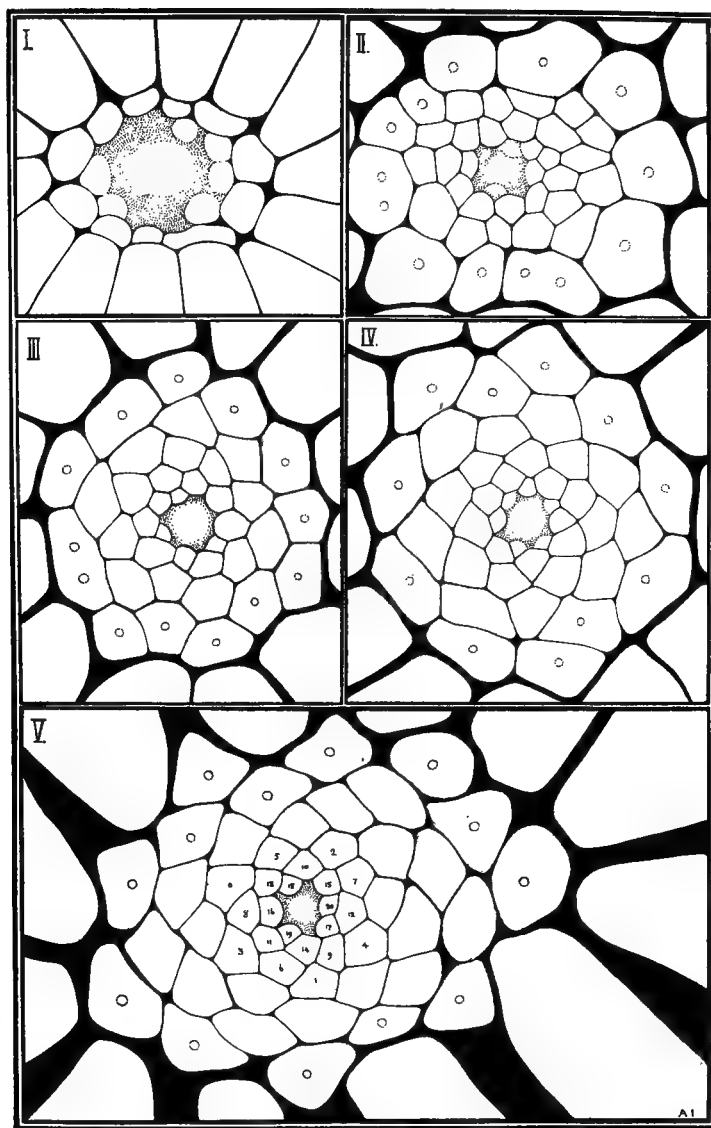
Fig. 86.—Transverse sections of the growing-points of young seedlings of *Pinus Pinea*:
I., II., cotyledons wholly enclosed in endosperm; III., IV., cotyledons emerging
from seed; V., cotyledons fully expanded, system becoming definitely (5 + 8).

have been wholly withdrawn from the testa and are beginning to expand, present a very remarkable appearance (fig. 86, II., III., IV.). Parastichies are still wanting, as indicating any definite system, and the primordia assume irregular forms under pressure ; so that the resemblance to a section of ordinary packed parenchyma is very close. Growth continues to be irregular in the individual primordia (III.), but as the plants become older it appears more regular and parastichies begin to appear. How far these appearances are partly due to irregularities in the phyllotaxis system itself is thus obscured ; but the irregularity in the phyllotaxis is associated with irregularity in the shape of the members. That the phyllotaxis system is itself irregular is rendered probable by the comparison of other types (*Cedrus Atlanticus*), but this would not necessarily lead to irregular shapes in the members. As the contact-parastichies become increasingly obvious, they give very anomalous results : for example, (IV.) is apparently a system (6+7) with irregular packing among the first leaves ; but when the cotyledons fully expand, and the plumule becomes visible between them, the presence of a definite system of the normal series becomes clear for the first time. The central portion of the bud is now unmistakably (5+8) (V.), although in the example figured this appears to have been only rendered normal by the opening up of a new curve by the member numbered 1.

Seedlings vary from (5+8) to (6+10), (5+8) being the usual type. Section

Fig. 87.—*Coleochaete scutata.* Young plant, showing radial and circular symmetry.

p 43

of a plant in which the primary shoot had reached the length of 6 inches, shows a normal (5+8) system with remarkable perfection, the members retaining to a very considerable degree the form of the quasi-square of the theoretical construction, owing to the very small extent to which progressive bilaterality has been carried. Such a bud, however, grown in a warm house, retains the primary construction to a much greater degree than the foliage-buds produced on older plants in the open air and exposed to desiccation : these primary shoots lacking the protection of the bud-system subsequently developed in the adult condition of the plant.

A very instructive case is afforded by the arrangement of the florets on bractless Composite capitula, and may be well observed

in large heads of *Cynara Scolymus* (fig. 53*b*). Here the primary members are entirely wanting, but their axillary shoots nevertheless present perfect curve-systems of constant (55 + 89) and falling
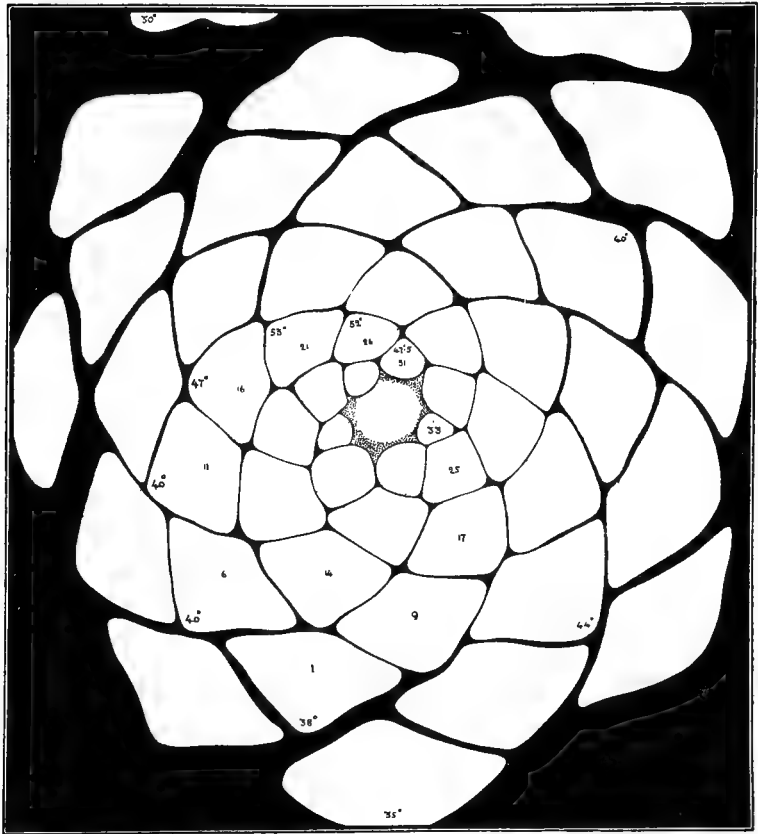
Fig. 88. — *Pinus Pinea.* Transverse section of the apex of the young seedling, 6 inches high : system (5 + 8).

systems (fig. 53*b*). That the growth-centres of the primary subtending leaves are actually existent, though they may not be visible, appears undoubted : their rate of growth has not become sufficiently great to raise them above the surface of

the inflorescence receptacle, and they remain so far *dormant growth-centres.**

But the discussion of the mutual relations of the florets of *Cynara* does not enter into the question of primary phyllotaxis at all, except in so far that it is a derivative arrangement, which follows the primary non-developed system so uniformly and closely that it may be taken as a perfect guide to the original construction. These florets, though not primary phyllotaxis elements at all, are not in any close lateral contact, but are packed round with hairs so that each develops independently and maintains its own normal orientation, without any angular alterations produced by mutual pressures. The curves are perfect Fibonacci systems, and two features of special interest may be noticed:—

    I. The rotation of the peripheral florets (fig. 53*b*) owing to secondary pressure against the smooth, firm involucre edge; no slipping is involved nor displacement, only a readjustment.

    II. The elongated oval shape of the ovaries, in the slightly spiral " median plane," due, again, not to any mutual pressure, but to the inherent structural tendency of two " median carpels" to build an oval rather than a circular organ.

Comparing *Helianthus* now with *Cynara*, it will be seen that the curve-systems are identically accurate in both types, but *Helianthus* differs (1) in having subtending bracts present and visible, although pressed out of their original positions by their axillary florets; (2) the ovaries of the florets are definitely rhomboidal by mutual pressure; (3) those of the decadent ray-florets change their shape but not their position, and thus become packed into triangular facets. The angular ovaries are of special interest: theoretically they should have presented the same oval shape as in *Cynara*, since they are constituted by the same two " median carpels." But in consequence of growth-pressure, each oval has

---

  * *Cf.* the interesting case of the missing subtending bract of the flower of *Nymphaea*; the axillary flower thus appears to fall in the normal phyllotaxis system, as if the flower replaced a leaf. But the young flower-bud does not fill the quasi-square left empty, and is packed into it with woolly hairs.

to fit into a square mesh of the phyllotaxis system together with the crushed subtending bract. The result is that the ovals with their long axis in the " median plane " of the flower are so adjusted that they come to lie obliquely across the quasi-squares, but without otherwise interfering with the curve construction. The radial extension of the ovaries, that is to say, breaks the long curves, giving them a serrated or *stepped* appearance, but the short curves remain unaffected.

This implies, however, no *displacement* whatever of the orthogonal construction system : the centres of construction remain unaffected, there is a change of shape, but not of position, so that the phenomenon is again not one of displacement but rather of readjustment.

Section of a young capitulum, for example (fig. 89), at the level of the style canals, gives a series of points which can be taken accurately for each flower ; the curves drawn empirically through these points show the theoretical square meshwork with as great a degree of accuracy as could be expected from a plant. The *displacement* of the florets is thus apparent and not real, and the effect of any radial elongation of members arranged in a spiral phyllotaxis series will be to *step the long curves*, while the short curves remain unaffected.

That some alteration in the phenomena of the curve-systems should therefore be observed in *Helianthus* in passing from the flowering condition with florets circular in section to the fruiting condition with radially elongated achenes, is sufficiently obvious.*
But such alterations have no reference whatever to the causes which produced the primary system of subtending bracts ; nor does such a phenomenon enter into the question of the primary importance of contact-pressures. The bicarpellary ovaries do not assume the flattened form in consequence of mutual pressure ; their flattened form is as much an inherent growth function as that of the two-carpelled fruits of the Umbelliferae : it is easy to see by cutting a capitulum in two, or by noting the shape of fruits adjacent to ovaries which have proved sterile, that the flattening of the fruit is quite independent of any pressures, although mutual pressures may make the angles more pronounced. The changes

* *Bot. Zeit.*, 1902, pp. 226, 230.

observed in the curve-systems are optical effects produced by
elongating the members of the system in a particular way, and the
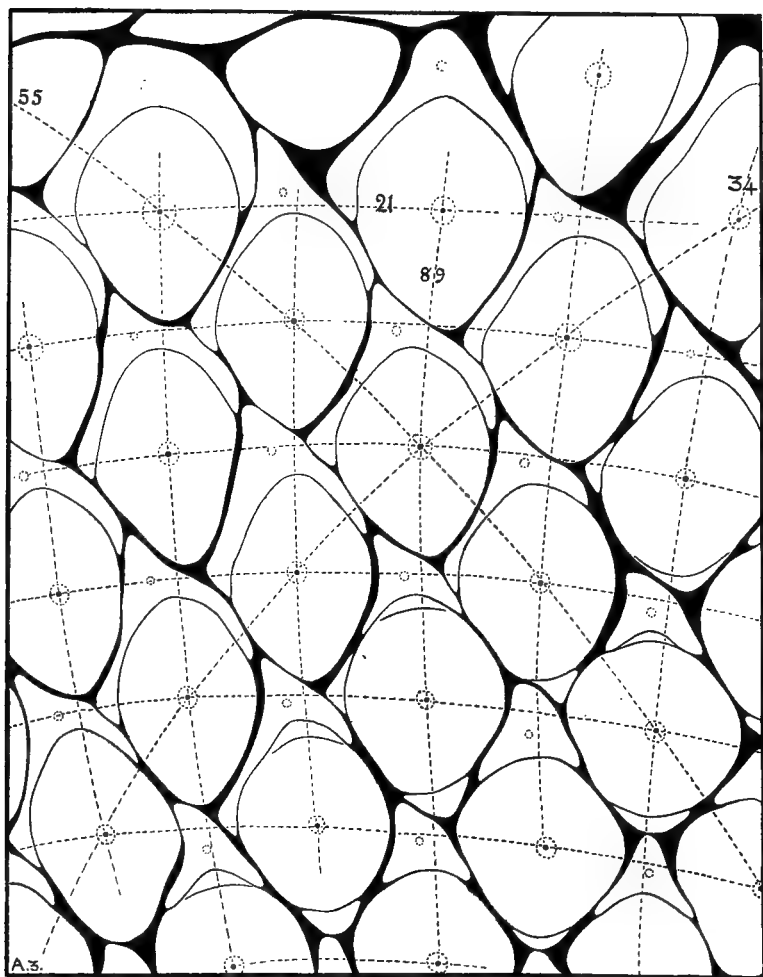
Fig. 89.—*Helianthus annuus.* Portion of a young 6-mm. capitulum, system
(34 + 55). Section at the level of the style canals of the developing flowers,
showing construction quasi-squares, and the oblique setting of the rhomboid
ovaries thus "stepping" the "34" curves. Quasi-squares of the comple-
mentary (21 + 89) system dotted.

amount of mutual pressure is determined solely by the relative
rate of growth of the receptacle and the fruits; and if the growth
of the former be only sufficiently active, contact-pressures would
be entirely eliminated.*

Fig. 90.—*Euphorbia Wulfenii*, Hoppe.   Terminal system of a strong shoot $(8+13)$,
showing progressive dorsiventral bilaterality of the members.

* A good example is afforded by the growth of the capitulum receptacle
in *Rudbeckia* and *Scabiosa*: *e.g.* in *Scabiosa atropurpurea* the florets form a
gradated series, but the fruits are required to be all the same size.   The axis

The change of angle observed in the intersection of the para-stichy curves of such inflorescences is thus due to the relative growth of the rapidly enlarging receptacle and its fruits. These changes are therefore t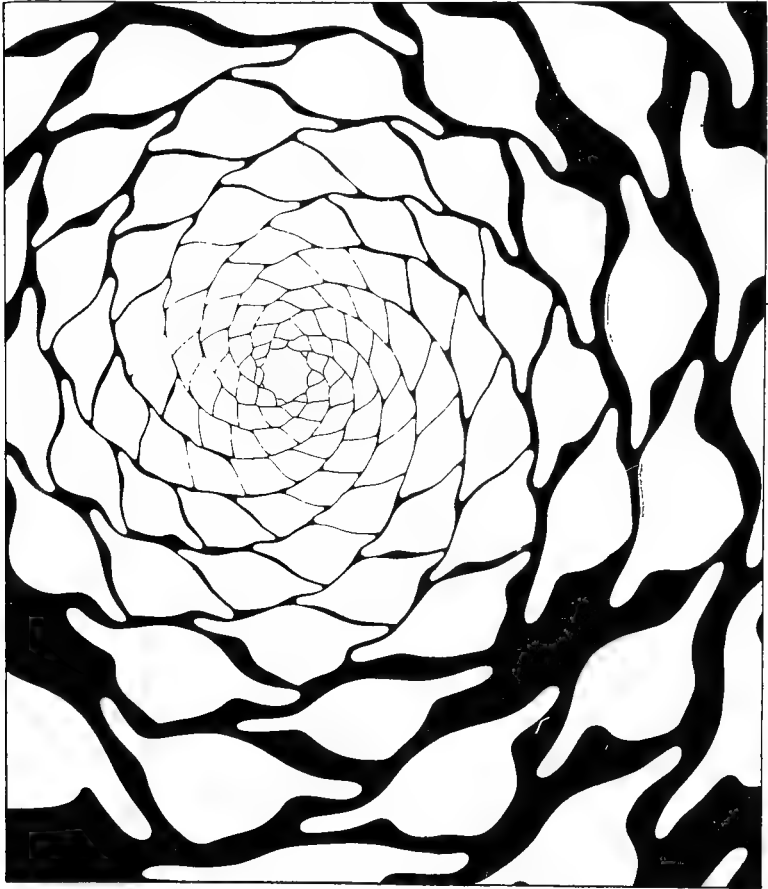ertiary effects in the phyllotaxis appearances, and are merely the expression of the mathematical properties of intersecting spiral curves, directly comparable to similar curve changes observed in shoots passing through a secondary zone of growth. Not only will any small amount of slipping of the angles of such ovaries, in the readjustment of radially elongated growth forms, tend to bring a third set of curves into view,* but the same appearance necessarily follows as soon as any growth change lowers the angle of the intersection of the contact-parastichies to 60° or raises it to 120°. These again are geometrical phenomena due to different rates of growth in a system which was previously considered to be adult, and have no bearing on the formation of the initial curve-systems observed in the first stage of development of the capitulum.

An identical phenomenon of growth adjustment, or " packing," occurs in the typical Aroid spadix, and is well seen in the case of the dimerous flowers of *Anthurium*. These inflorescences, like *Cynara*, possess their bract growth-centres clearly existent and functional, although, save for exceptional cases such as *Acorus*, they are only traced through the intermediary of their axillary flower-shoots ; and these in many species (*cf.* fig. 93) present a normal curve-system of $(8+13)$. But the dimerous flowers of *Anthurium*, $(2+2)$ in construction, and orientated in the " median plane," present two outer perianth segments as the first-developed members, and hence in a growing system these will be larger than the others, so that the flower is always slightly elongated in the " median-plane," that is to say, approximately along the long axis of the spadix, and presenting a radial extension of the

elongates in compensation sufficiently to loosen all contact-pressures, but the curve-systems remain undisturbed ; although a new set of spirals may appeal to the eye, owing to the large relative size of the *involucels*. Hence a lateral $(8+13)$ capitulum becomes $(5+8)$ in the fruiting condition.

* When the long curves become thus stepped, and so tend to be less conspicuous, a $(34+55)$ system is readily confused with a $(55+89)$ in the latter fruiting condition. *Cf.* Jost, *Bot. Zeit.*, 1902 ; Leisering, *Prings. Jahrb.*, 1902.

floret. It would therefore be expected from theoretical construction that the long curves should prove to be *stepped*, owing to apparent displacement, as the lozenge-shaped flowers readjust to fit into the square meshes of the system.*

Comparison of fig. 93 shows that such is the case; the 8-curves are slightly stepped, but the 13-curves run clean-edged. At the apex of the spadix the phyllotaxis system falls normally to $(5+8)$, and here again the 8-curves are the smooth ones, while the 5-curves are stepped.

In the case of *trimerous* flowers, similar secondary relations between the florets produce phyllotaxis effects, which again have little bearing on the primary construction system, in that the trimerous flowers produce a secondary appearance of hexagonal facets which therefore present three lines of contact; this being again the general case for trimerous Monocotyledonous types (*Acorus, Muscari*). In dealing with examples of hexagonal facetting it must, however, be clearly borne in mind that *hexagonal facetting* has no necessary connection with *hexagonal packing*. Hexagons which appear very fairly regular may still be orthogonally arranged. By taking a normal orthogonal $(8+13)$ system (fig. 95), and cutting off corners at the point of contact, *i.e.* by pressing the members against each other instead of sliding them, an orthogonal series of hexagons may be obtained, which show a third line of contact according to the mode of operation, 5/8/13 or 8/13/21/; the latter being shown in the figure, which is designed more particularly to illustrate the relationship of the prismatic cone scales of *P. Pinea*.

* *Cf.* Schwendener for Displacement Theory, in Goebel's *Organography*, Eng. trans., p. 80. This does not account for the whole of the phenomena : the adult florets are almost square lozenges (*cf.* fig. 93), and the greater part of the slip is now due to the radially symmetrical *orientation* of a decussate $(2+2)$ system, individual florets being constructed in median and transverse planes. The effect noticed being thus connected with the subject of the orientation of *lateral axes*, can with difficulty be included under the heading of Phyllotaxis ; but it is sufficiently clear that though helical curves may intersect to give square facets, it is only when the number of curves in either direction is equal that the diagonals of the facets will be median and transverse planes and no readjustment will be necessary (*cf.* fig. 110, chap. vi.).

All these hexagonal structures are, however, secondary productions in the phyllotaxis system; another example of primary hexagonal leaf-facetting is afforded by *Euphorbia mamillaris* (fig. 92).

> This plant is of further interest in that, as in analogous ridged Cactoid forms, the phyllotaxis is anomalous: *e.g.*, the specimen figured was 7-ridged $=(3+4)$ system at the level of the soil, but after the production of about 300 members, two new curves are added quite irregularly (fig. 92*b*), and the system becomes $(4+5)$ or 9-ridged, this formation being continued to the apex for over 500 members. The new curves are interpolated without rule, and the lateral branches commence as $(2+3)$, which again soon rises to $(3+4)$.

The case of the *Pinus* cone (fig. 7) is of interest, again, in that the rhomboid scales are not leaves but secondary structures obeying the same laws of uniform growth as their reduced parent members; but these cone-scales are not elongated radially like the *Helianthus* ovaries, but tangentially. The converse phenomenon will therefore be observed in the phyllotaxis pattern; that is to say, the long curves will now remain clear, while the short curves will exhibit stepping. The readjustment of a tangentially elongated member in the square meshwork of the growth-system thus tends to change the shape but not the position of the member. Such tangential extension, again, becomes the normal condition in all "dorsiventral" foliage-leaves, and will be considered again from another standpoint. The essential point at present is to note that such readjustments, and sliding-growth effects, do not imply any *displacements* of the growth-centres. The primary phyllotaxis relations are unaffected, and any secondary appearances which may be involved in the pattern follow geometrically from the properties of intersecting spiral curves. All contact-pressures must be growth-pressures, and must be studied, therefore, from the standpoint of growing systems.

Schwendener's Dachstuhl theory, as a working hypothesis, thus disappears as completely as the original one of Schimper and Braun it was designed to correct. Apart from the mathematical conception of helices inherited from these botanists, it was founded on two perfectly definite facts of general observation :—

(1) The contact-relations of the young primordia.

(2) The fact that an actual displacement of the corners of members growing in close contact does take place.
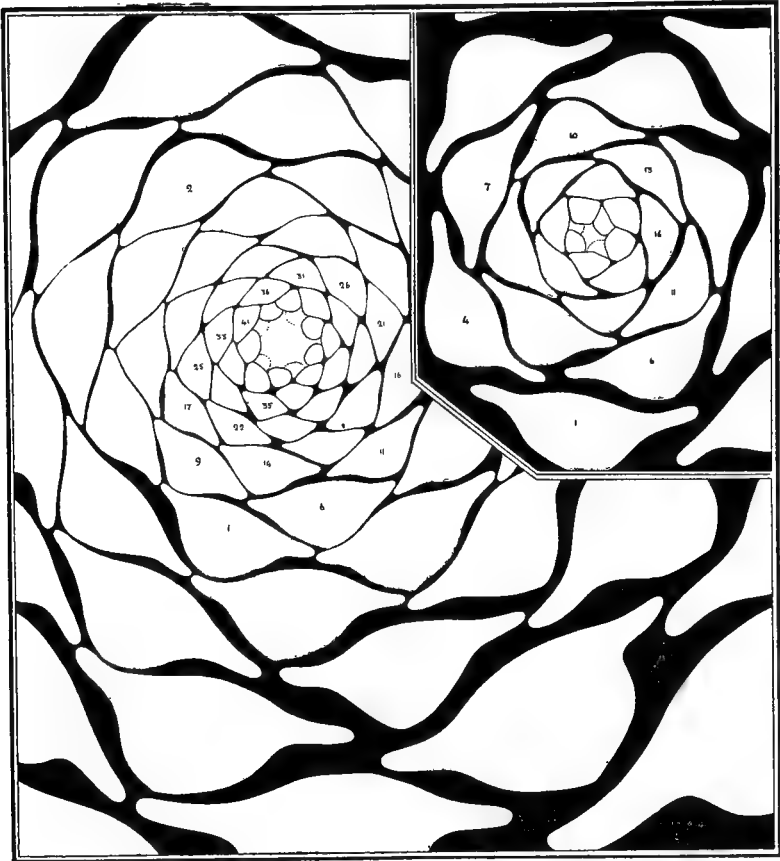

Fig. 91.—*Euphorbia Wulfenii* (Hoppe).   Terminal system of weaker shoots, $(5+8)$ and $(3+5)$.

From the literature of the subject (Schumann, Schwendener, Jost), it is clear that it is impossible to prove the first point of contact-relation to the satisfaction of all, since many cases occur in which the question of lateral contacts would be described differently

S

by different observers. The fact remains that in many cases the primordia not only do not appear to touch, but are certainly not in any relation of mutual pressure (*Aspidium*). While this standpoint of origin in contact creates a prejudice in favour of regarding the primordia as of a bulky nature from their first inception, the growth-theory here proposed, by postulating an initial growth-centre of the nature of a mathematical point, leads directly to the view that contact-relations are secondary, and that theoretically growth must proceed around each centre until it reaches the field of adjacent growth-centres, although the actual boundary may be beyond observation. What is really established by the observations of Schwendener is the fact that these contact-relations are characteristically of a special type, to which the conventional terminology of a " concentrated system " has been applied. It is clear, however, that the growth-centres of the primordia are always quite distinct from each other, and that the contact-relations must be ultimately produced if growth only continues long enough, and in the great majority of leafy shoots contacts are soon established. But such contacts will not necessarily imply any displacements, and the phenomena of displacement of the edges of the members according to a definite plan is perhaps one of the most remarkable features of ordinary spirally constructed leafy shoots ; and there can be no doubt that the existence of such slipping or sliding-growth effect, which apparently implies a forcible displacement of the members, was the fundamental fact which led Schwendener to postulate a forcible displacement under mutual pressure. The actual significance of the *regular displacement* of leaf edges in *asymmetrical systems*, which it must also be noted does not take place in symmetrical constructions, may be left for the present, since it only becomes apparent from the mathematical considera-tion of the subject. It is only necessary to point out that the necessity for such displacement naturally follows from the general conception of a phyllotaxis system as built up of primary and secondary growth-centres, and the fact that the required dis-placement effect does occur is one of the strongest proofs of the practicability of the log. spiral theory (*cf. Mathematical Notes*).

PLATE XXVII.
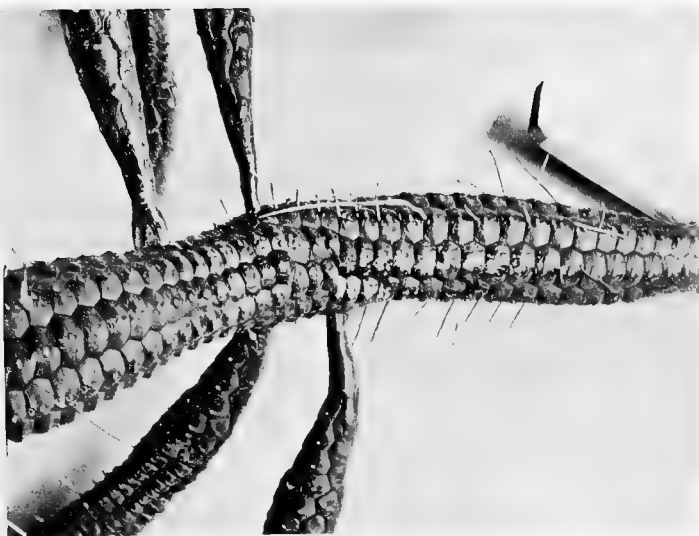
Fig. 92b.—*Euphorbia mamillaris.* Branching shoot, showing anomalous introduction of new curves, indicated by the forking of the lines of hexagonal facets.

Fig. 92a.—*Euphorbia mamillaris.* Apex of shoot, system (4 + 5), showing leaves on hexagonal facets : 20 mm. diameter.

PLATE XXVIII.

Fig. 93.—*Anthurium crassinervium.* Spadix 12 mm. in diameter, system (8+13), reduced at apex to (5+8).
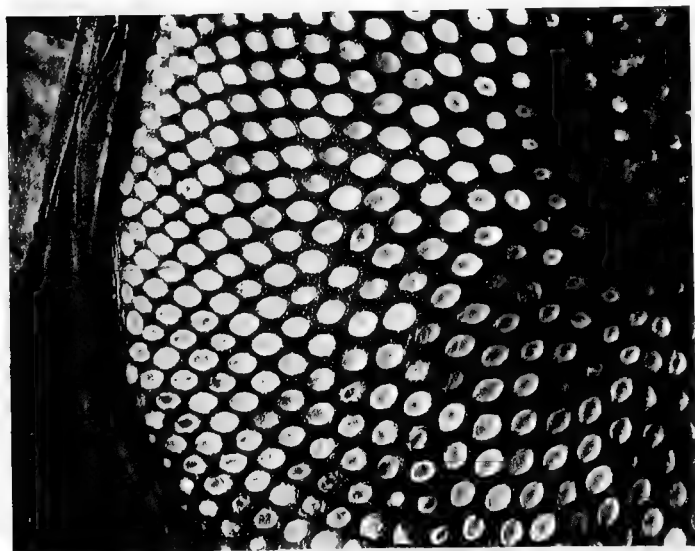
Fig. 53b.—*Cynara Scolymus.*—Portion of capitulum.
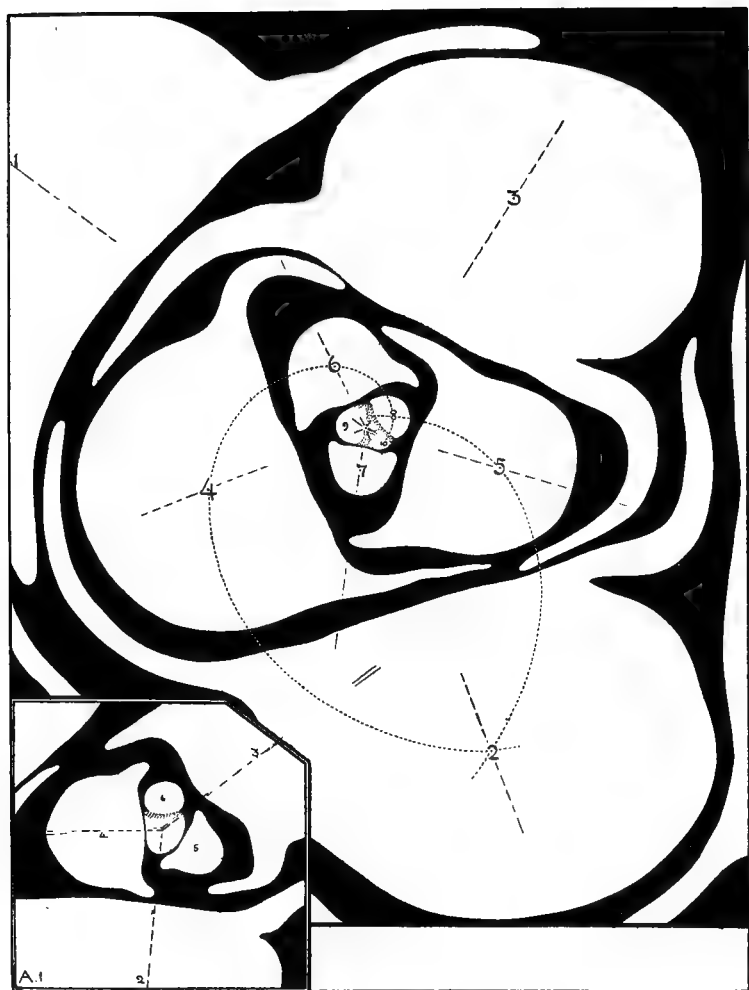
Fig. 94.—*Nymphœa alba*, perennating bud of year-old seedling, 3 mm. in diameter, system (2+3). Transverse section for measurement of the divergence angles on lines drawn through the xylem of the small bundles.
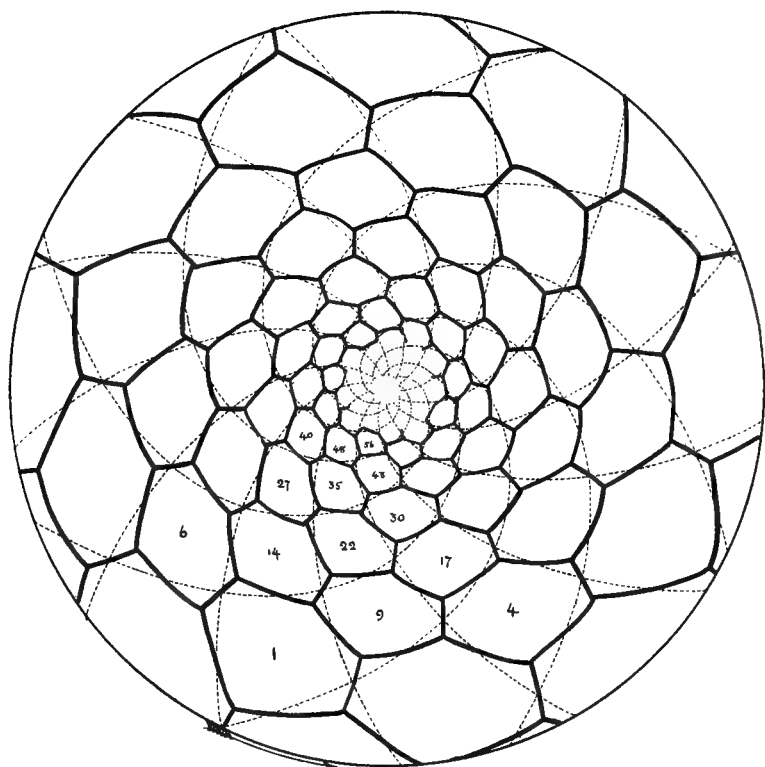
Fig. 95.—Geometrical scheme (8 + 13) for formation of hexagonal facets in an orthogonal construction.

IV. Eccentric Growth.

THE special type of symmetry observed in a plant body which presents a distinct upper and under surface, differing in appearance and physiological function, has been very generally described by the term *dorsiventral* (Sachs). This term, borrowed from the usage of Animal Morphology, in which this type of symmetry is the rule rather than, as in plants, the exception, naturally implies the possession of a *dorsum* and a *venter*, or at least a hypothetical plane dividing the body into two regions which will ultimately become these surfaces. Even in Zoology the convention is admittedly based on the body structure of higher animals, and from these is carried down to less differentiated types, as implying a certain *bilaterality* of structure. In its application to Botany, therefore, in the absence of anything which corresponds to either *dorsum* or *venter*, which appear to be regions ultimately correlated with the evolution of a locomotile body seeking solid food, the term must remain a purely metaphorical expression; and, as in the case of all borrowed terms, care must be taken lest the suggested analogy be ultimately accepted as an actual fact. The term *dorsiventral* apparently presented itself to Sachs in preference to the simpler term *bilateral*, in that it contained the suggestion that the two surfaces must be dissimilar; and the wider term *bilateral* would, according to him, include the case, for example, of an erect shoot bearing members in two rows, or with what has been previously termed a symmetrical $(1+1)$ construction. For the same reason a diarch root would be bilateral, though few would nowadays object to a diarch root being still classed as only a special case of radially symmetrical root construction. In

Animal Morphology, again, the conception of an *axis* and its *appendages*, though admittedly a convention, is based on the simple fact of observation that in higher animals the body is constructed of one main axis and its limbs, or in Arthropoda, for example, of one main axis and segmental appendages. The fact that the main axis exhibits dorsiventral symmetry leads to the application of the same theoretical conception to the symmetry of the appendages. But the term *dorsiventral* is an *axial* designation; the idea of an appendage being dorsiventral in itself is wholly outside the range of the convention. Thus, while the transference of the term *dorsiventral* as a *metaphor* to a special case of shoot symmetry may prove helpful, its common application to the case of a *bifacial* foliage leaf, which is typically an appendage borne on a radially symmetrical axis, remains open to grave objection. Similarly, the extension of the term to special floral systems (inflorescences), and even to zygomorphic flowers (Goebel),* may be of very questionable advantage; since the application of a metaphor to constructions in which it is not otherwise the custom to discuss the dorsal and ventral surfaces, adds little to descriptive power; while there is no obvious criterion as to which surface is to be regarded as the dorsal and which the ventral, and further conventions require to be introduced. Sachs first pointed out the fact that the so-called dorsiventrality of shoots as a type of morphological construction was correlated with a difference in physiological reaction to stimuli : the change of symmetry being the outward and visible sign, or even the cause (*Physiology*, pp. 489 and 493), of a fundamental change in protoplasmic reaction, and that dorsiventral shoots were plagiotropic. The special case of *isobilateral* leaf-members here again presented an objection to the use of the wider term *bilateral*; while *bifacial*, on the other hand, scarcely conveys the impression of a dorsiventral shoot

---

* According to Goebel, the term *dorsiventral* implies an upper and an under side, while the conception of *zygomorphy* is based on a *subordinate feature*, the existence of a right and left side ! Both phenomena are obviously equally the consequence of *eccentricity*, the primary feature being the displacement of the growth-centre, from which all secondary phenomena of "irregularity" or asymmetry naturally follow.

which may still be practically circular in section. The term *dorsiventral* thus became applied by Sachs as indicating a definitely physiological conception of plant symmetry, which might be expressed by a morphological *bilaterality*, but the bilaterality must not be " double," that is to say, a dorsiventral organ must have two unlike surfaces.

It is clear that not only have several special cases been included under the same terms, but the existing terms are not very strictly defined. Thus the case of a symmetrical $(1+1)$ leafy shoot presents little difficulty ; there is no need to regard it as bilateral any more than a $(5+5)$ shoot would gain by being called tensided. The cases of the *cladode* and the *fasciated* stem are again only special cases of radial symmetry, while the latter has much in common with the often-quoted type of *Marchantia* and Algal forms, as *Fucus*. Two cases remain, the *bifacial* foliage leaf, and the " dorsiventral " shoot bearing leaves on the so-called dorsal surface : the former presenting a phenomenon which is the property of an appendage without reference to the symmetry of the axis bearing it, the latter a special case of axis construction. In fact, it now becomes apparent that the so-called dorsiventrality of these structures may be due to entirely different causes, and that two distinct phenomena have been included under the same metaphorical expression. The bilaterality of an appendage is a mathematical property of the primordium, and may be expressed as either a *bifacial* or *isobilateral* flattening ; while the so-called dorsiventrality of a leafy shoot system is merely the expression of its structural *eccentricity*. The term *dorsiventral* may be therefore conveniently eliminated from botanical phraseology altogether ; the physiological conception of Sachs being clearly defined by his later expression *plagiotropism*. At any rate, before committing oneself too far to the pursuit of academic abstractions as to the symmetrical relations of living and growing organisms, it will be well to consider the mathematical consequences of certain simple types of growth.

Returning to the original proposition of growth, it is obvious that mathematically centric growth is only a special and ideal case, which is possibly extremely rare in nature. If perfect radial

growth at a uniform radial distribution from a growth-centre implies the uniform action of various surrounding stimuli, which in the vast majority of cases are unequally distributed, the wonder remains that centric growth should be on the whole so closely approximated that it appeals to the senses sufficiently to justify this simple mathematical conception as a general starting-point. Thus, although the majority of tree trunks and branches may be fairly circular in section, few would show an even approximately central pith, while the eccentricity of large starch grains becomes the type. That the growth-centre of a shoot exposed to varying environment should become eccentric is therefore not to be wondered at; but the degree of eccentricity can only be judged by the after effects and by the eye, so that a slight alteration of the system would not necessarily be noticed, and it becomes very difficult to draw any sharp line between what may be taken as sufficiently centric and constructions which are obviously eccentric.

Such cases of eccentricity and their relations as expressed in the phyllotaxis systems may, however, be as readily followed by geometrical constructions as the allied cases of the centric and eccentric tree trunk, or the centric and eccentric starch grain, the construction lines of which are generally accepted as being represented by orthogonal trajectories (Sachs), though it is true that no absolute proof has yet been given. Further, it becomes possible, by geometrical constructions similar to those already put forward as explanatory of the relations of symmetric (whorled) and asymmetric (spiral) *centric* phyllotaxis systems, to deduce the properties of the same system when the whole growth-system becomes eccentric: the whole series of phenomena representing, in fact, definite mathematical cases of growth construction which would naturally be expected to occur in organisms exhibiting growth under different aspects.

Just as, in dealing with the growth and phyllotaxis of the main shoot axis, the chances would appear to lie mathematically in favour of asymmetry rather than symmetry as the fundamental case, so that perfectly symmetrical construction, as exhibited in the $(2+2)$ or decussate system, or the $(5+5)$ symmetry of flowers,

is probably to be regarded as a special case of construction evolved by secondary specialisation for a special set purpose,—the existence of a capacity for becoming symmetrical being the essential character which may be increased by natural selection,—so again, in the case of centric and eccentric construction, a tendency toward *eccentricity* would be expected, in that it presents the most general mathematical construction ; while the chances that nutrition or circumstances of environment would not be absolutely constant on all sides of the organism are enormously greater than those of uniformity.

The essential question is rather, Is there such a thing as absolutely centric growth at all in nature ? Hypotheses of centric growth have been read into the plant as presenting simple mathematical cases ; but should not the eccentric be rather taken as the starting-point, since, by assuming a simple case which is not the primitive one, the subject may be approached from a misleading point of view ? The marvel is, in fact, not that some shoot systems should show marked eccentricity of growth, but that any should ever approximate the centric, *unless the inherent growth faculty of the organism in working out its specific form according to simple laws of growth is, as a rule, far stronger than its tendency to respond to external stimuli.* However, the fact remains that the difference between centric and eccentric growth phenomena is only loosely judged by the eye, which is not a mathematical guide, and for practical purposes growth is often so approximately centric that there is no harm in calling it so, so long as it is remembered that it is not possible to draw a sharp distinction between the two cases by actual observation.

So far as eccentricity of growth may be induced by inequality in the action of external stimuli, such as light and gravity, quite apart from the equally possible conception of inherent irregularity of construction, it becomes clear that every lateral flower shoot, borne on an erect axis, would have a natural tendency to become eccentric, just as every lax shoot which is not strong enough to support its own weight. A tendency to more or less obvious zygomorphy should, for example, be the rule in any short lateral floral axis, and not the exception ; and here again with no reference

whatever to special external agencies such as insect visitors, but simply as a structural feature. Natural selection may increase this tendency, but it was always present in the growing-point of the shoot. By stating the converse for " terminal flowers " on centric shoots, one begins to arrive at the truth underlying such generalisations as that of De Candolle that no zygomorphic flower could be terminal, notwithstanding the fact that every flower terminates its own axis.*

It is also a point of interest that the more general occurrence of eccentric growth in flower shoots, in that it involves the subjective appearance of a certain bilateral symmetry, is responsible for the introduction of conventional conceptions of "median planes," etc., which, though transferable to symmetrical phyllotaxis systems, have absolutely no existence in the more generalised case of asymmetrical construction.

Because the genetic-spiral of Schimper would not explain the phyllotaxis of a dorsiventral shoot, Sachs was willing to throw over the entire spiral theory, although he was fully aware of the fact that cases of markedly " dorsiventral " phyllotaxis are relatively few, occurring usually in growth constructions specialised in other directions; and the elucidation of such " dorsiventral " constructions remains a test case for any suggested hypothesis which claims to interpret the facts of shoot construction and leaf arrangement. The present standpoint is sufficiently clear; there can be little doubt that the habitual use of the term " dorsiventral " introduces a fallacious standpoint; one incautiously argues that the distinction of a dorsal and ventral surface as in an animal must be a very remarkable specialisation, and so undoubtedly its consequences appear in the adult shoot, though the separation of the two surfaces is not apparent at the growing-point where the construction commences. Once the term " dorsiventrality " is eliminated, or only retained as a harmless metaphor, and it begins to be obvious that all that the phenomena include is an unequal distribution of growth in different directions, the subject becomes much clearer from the point of view of strict morphology; while the physiological conception of plagiotropism, and whether this is

* Cf. Goebel, *Organography of Plants*, Eng. trans., p. 133.

the cause or the effect of the unequal growth, may also be placed on one side.

The log. spiral hypothesis, based on the laws of uniform growth, which so readily established the connection between spiral (asymmetric) and whorled (symmetrical) *centric* leaf arrangement, is equally readily applicable to the case of *eccentric growth-systems.* The eccentricity involves the whole growth-system of axis and appendages (leaves), and the mathematical properties of the quasi-square systems remain unaffected, the only alteration produced being a co-ordinated change in the form of the whole shoot-system ; just, for example, as in the case of an unequally developed Pine-cone, every scale on the cone is affected, and takes its share in the structural eccentricity.

Just as uniform centric growth is a definite mathematical conception, the geometrical properties of which may be readily investigated by drawing suitable log. spiral constructions on a groundwork of a circular meshwork of quasi-squares, and the geometrical properties of such constructions may be deduced before making any further observation of the plant; so it is well to put together the general facts of the homologous cases of eccentric growth, in order to see what phenomena will be characteristically expected, before any attempt is made to bring plant constructions into line with such a hypothesis.

The difficulties in the way of getting a satisfactory geometrical construction for an eccentric growing system, in which, that is to say, the eccentricity is progressive, and becomes more marked as growth proceeds, although it may not be visible to the eye to begin with, are naturally considerably greater than in the first-studied simple case of centric distribution (fig. 24); since all the periclinal curves in the most general case would cease to be circles, and become complicated ovoid curves very much of the type observed in typical starch grains, while the diagonal construction lines cease to be log. spirals, although all the lines may still be regarded as derivatives of these curves. A useful figure which appears to combine all the essential facts of eccentricity, together with a simple geometrical method of construction, in that it is wholly constructed in terms of orthogonally intersect-

ing circles, may be adapted from a special case of electrical distribution.*

Such a diagram is then an eccentric homologue of fig. 24, and any phyllotaxis system for uniformly progressive eccentric distribution may be taken from it. It must be noted, however, that although a diagram in terms of circles has been utilised because it is easier to construct, there is no suggestion that the circle represents the true shape of the periclinal curves. This diagram is a special case, and is only taken so far as it goes, in that it will give the correct appearances within the error of estimation by the eye, and is, at the same time, a mathematically correct orthogonal

---

* For the construction of this figure I am indebted to Mr E. H. Hayes. It represents one half of two systems of coaxial circles which intersect orthogonally, which would represent in electricity the lines of magnetic force around two equal and parallel currents travelling in opposite directions. The data for drawing it are as follows :—

Let XX' and YY' be rectangular ordinates intersecting at the origin O. From O along the axis OX take a point C, 5 inches from O. The centres of the intersecting circles fall along CX and OY, OY' at the following distances. C = the centre of construction, on OC produced describe circles with centres . . at distance from C . . . with radius.

3·399 inches .	6·749 inches.
1·565 ,,	4·255 ,,
·778 ,,	2·896 ,,
·401 ,,	2·041 ,,
·210 ,, .	1·464 ,,
·111 ,, .	1·059 .,
·0588 ,, . .	·769 ,,
·0313 ,,	·560 ,,
·0167 ,, .	·409 ,,
·0089 ,, .	·298 ,,
·0047 ,,	·218 ,,

The intersecting circles pass through C with centres on YY' at distances from O of

±1·625 niches.
3·633 ,,
6·882 ,,
15·388 ,,

also the circle through C with centre O, and the straight line OC. With these data, intermediate meshes may be filled in empirically within the accuracy of drawing the figure.

system of quasi-squares. Since, again, an eccentric system in which growth is unequally distributed on different sides conveys to the eye the subjective appearance of a *displacement of the growth-centre* towards one side, while the general approximation to a circular outline may not be affected, it may be convenient to make use of this phraseology as a simple way of describing the construction, although it has no causal significance. For example, by selecting the $(5+5)$ system of construction curves a figure will be obtained (fig. 96) which is an eccentric homologue of fig. 55, and represents definitely, therefore, the general construction mechanism of a zygomorphic pentamerous flower. In this special case the growth-centre has apparently been displaced towards the upper surface (posterior side of the floral diagram); the converse construction is seen on turning the figure the other way round.

The diagram will now be seen to illustrate several points of interest which will be useful in the interpretation of floral construction :—

I. The system has lost its radial symmetry and become definitely bilateral, or, as it has been termed, "dorsiventral" ; that is to say, as soon as the growth-centre is displaced, a line may be drawn dividing the construction into two halves as a simple geometrical consequence of the eccentricity.

II. Notwithstanding this the construction remains definitely $(5+5)$; that is to say, all previous deductions based on the corresponding centric type continue to hold. The system is *growing*, and the growth-centres in each whorl of five are still *initiated simultaneously*: the fact that they may afterwards grow at different rates is wholly secondary.

III. But while the strict alternation, the contact-relations, and the simultaneous initiation of five new centres remain unaffected, the appearance of the system at any given moment will always present the subjective effect that the largest members must have started first! Each cycle of five has in fact been described as a "successive whorl"; while a construction of the type of fig. 96 would be termed "ascending development," and its inverted homologue a case of "descending development." It is at once clear that a "successive whorl" is a contradiction in terms, and

that accepted interpretations of the facts of ontogeny are very conventional.
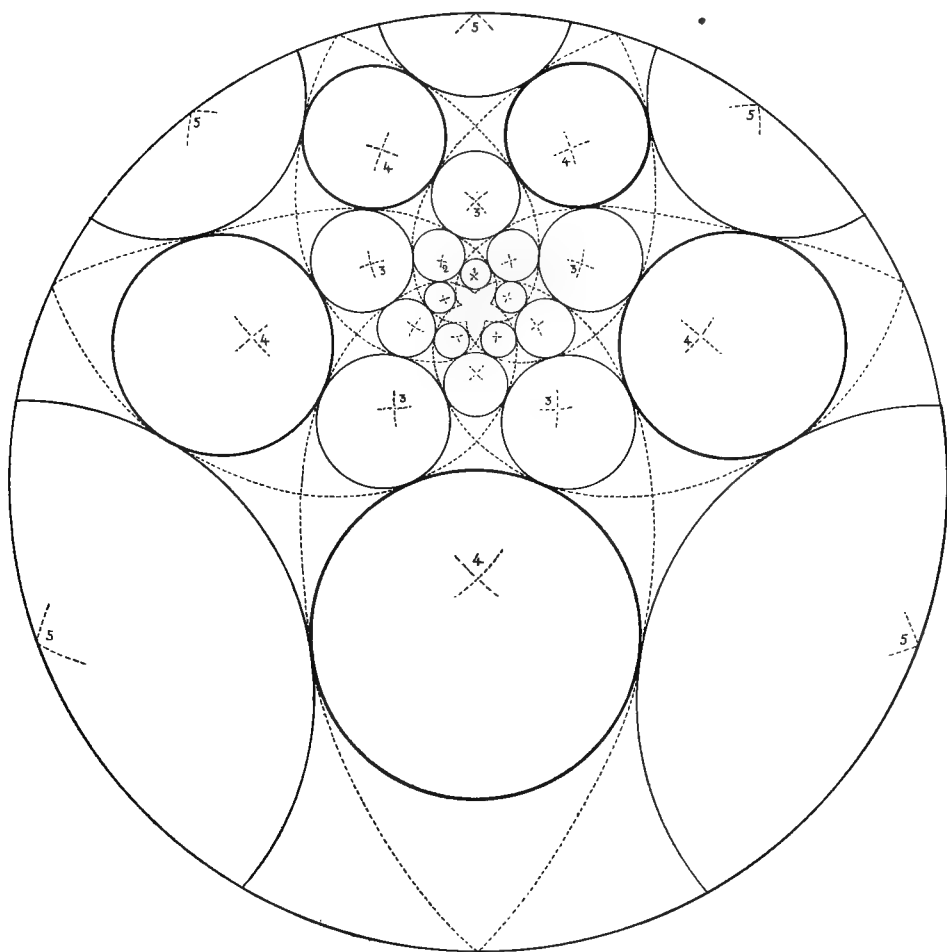
Fig. 96.—Eccentric growth ; system (5 + 5).

IV. The essential point in such a construction is that the eccentricity is *progressive*, and is therefore increasingly obvious at the periphery of the figure, while towards the centre it may be

indistinguishable from centric growth. A developing shoot-system, that is to say, may be so approximately centric in the region of the growth-centre that it may appear perfectly normal to the eye, and yet a very obvious amount of inequality may appear in the older members.

Fig. 55.—Centric symmetrical construction (5 + 5).

V. The lateral members themselves share in the distortion, in that the ovoid-curves which fit into the quasi-squares are no longer symmetrical in themselves unless they fall in the new plane of bilaterality. That is to say, the members proceeding from the sides of the system will themselves be asymmetrical; or, in tech-

nical phraseology, *anisophylly* is a necessary accompaniment of " dorsiventrality."

The subject of anisophylly (Wiesner, Goebel *) is, however, a very wide one, and no more is intended at this stage than the indication of the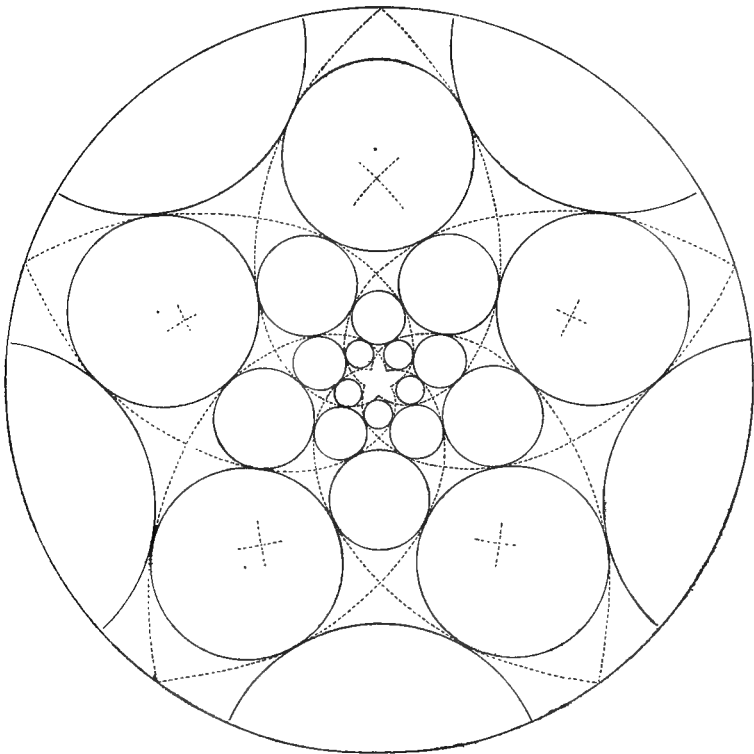 fact that all such cases of asymmetry require to be studied from a definitely *structural* basis; * and that anisophylly is a necessary consequence, both in the form of unequal leaf-members (Wiesner) and unequal-sided leaves (Goebel), just as in the corresponding case of the formation of the lateral pinnules of a compound leaf. And further, the study of eccentric growth phenomena affords a guide to the type of anisophylly to be expected, that is to say, to the fundamental and primary form of anisophylly, any variations from which must be regarded as secondary specialisations. For example, if the limiting log. spiral curves of a $(1+1)$ mesh (fig. 24) be taken as possibly representing a general fundamental symmetrical growth-form for a leaf-lamina, of which asymmetrical homologues would be produced by unequal rates of growth of the general form of the asymmetrical curves used in plotting an asymmetrical construction, the alteration of such a symmetrical form consequent on its development in an eccentric growth-system should be similarly expressed by the curves bounding the quasi-squares of the eccentric system. Such a suggestion, based on the standpoint that the fundamental growth-form of the typical leaf-lamina (the *Urblatt* of Goëthe) is to be derived from a unilateral retarded growth distribution initiated from a basal growth-centre on the surface of the axis, is purely tentative; but the homologues of the log. spiral curves of the centric $(5+5)$ system, seen in fig. 96, serve to indicate with sufficient approximation the general fact that the lateral leaf-members of an eccentric growth-system must themselves be asymmetrical, and only those which develop in the plane of eccentricity truly equilateral. The anisophylly, again, is of the general type that the largest side of the leaf is on the side of the

---

* *Cf.* Goebel, *Organography of Plants*, Eng. trans., p. 99: "Anisophylly occurs exclusively on plagiotropous shoots and is a *character of adaptation* which has an evident relation to the direction of the shoot and especially its position with regard to light."

axis showing the greatest growth; and when, as is so commonly the case, the displacement of the growth-centre is toward the upper side of the shoot, the largest side of the leaf, as also the largest leaves, will be toward the lower surface.

Similar generalisations apply to the structure of leaf-pinnules, in which the largest lobe is necessarily on the side nearest the base. This was, in fact, the conclusion reached by De Candolle from empirical observation, and may be taken to indicate that the great majority of cases obey these structural conditions. The reverse effect does, however, occur in a few cases, notably in the example of *Goldfussia,* a decussate type,* and to these the teleological explanation may be more safely applied: the only point to which attention is directed at present being that such apparent exceptions do not disprove the general mathematical basis of the construction mechanism. Teleological interpretations which seem to satisfy some cases but not others are never wholly satisfactory; but that secondary specialisations may be super-imposed on the primary construction would be naturally expected.†

* *Cf.* Goebel, *Organography,* p. 112.

† As an example of a comparable phenomenon in which the primary condition of eccentricity is apparently reversed by a secondary specialisation which takes the form of a later development of eccentricity in a diametrically opposite direction, the case of the development of the typical Papilionaceous flower may be taken, and the same holds for many cases of specialised zygomorphic flower-shoots. Thus, in *Cytisus Laburnum,* longitudinal sections of the perennating buds in January show that all the floral members are laid down in position on a markedly eccentric receptacle; the anterior side being twice as large as the posterior, the anterior members also exaggerated; so that the conventional interpretation of ascending development is obvious. The same eccentricity persists on until the anthers are fully formed and the ovules produced inside the carpel (March); but as the mechanism receives its final adjustment in the colouring buds, the growth of the posterior side of the flower is considerably increased, *i.e.* the eccentricity is reversed, and the posterior petal becomes the largest, and the posterior side of the receptacle is thrown up as a considerable elevation, giving the axis that semi-crateriform condition which has induced systematists to describe the type as "perigynous."

Similarly, in *Viola odorata,* longitudinal sections of young buds cut in March show all stages in floral development, and may be accurately plotted by cam. lucida. The same phase of "ascending development" indicates a structural eccentricity in the system, and is also expressed in the unequal development of the floral receptacle, the anterior side being again considerably larger than

T

The general application of this assumption of anisophylly in the phyllotaxis system is plotted in fig. 97 for the simple decussate
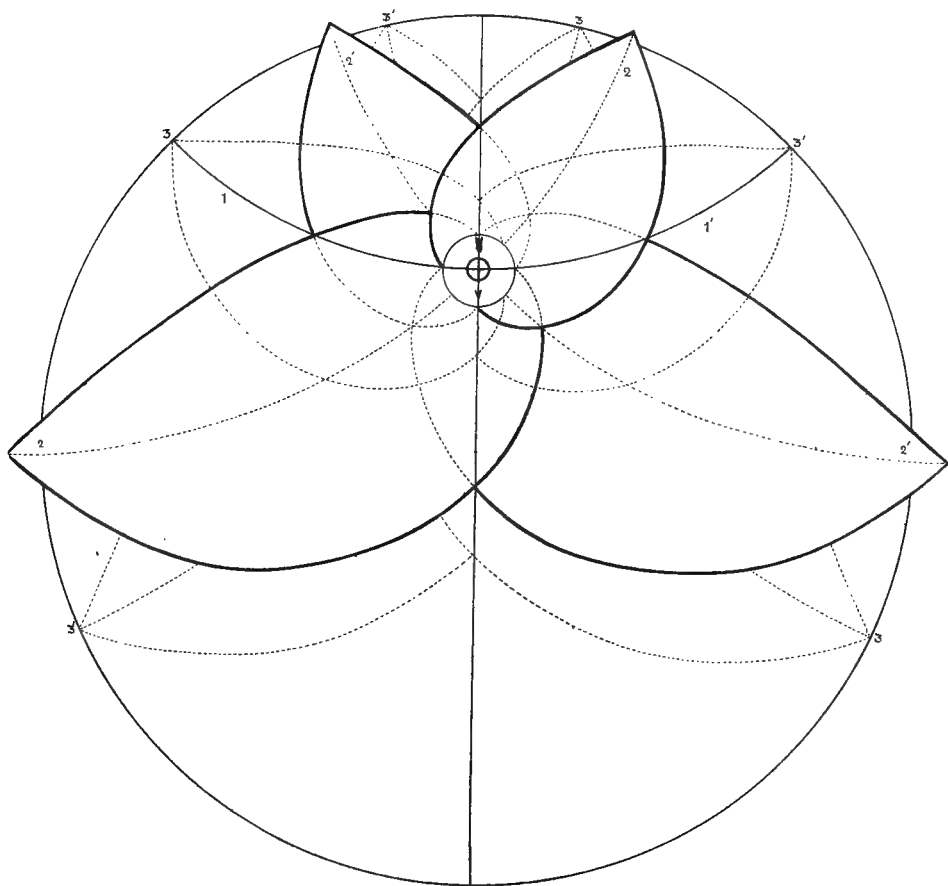
Fig. 97.—Eccentric growth, system for orientation and approximate anisophylly of the members of (1 + 1), (2 + 2), and (3 + 3) systems.

the posterior. At a slightly older stage, when the flower stalk is 2 mm. long, the construction appears equalised, and the receptacle takes on a uniformly crateriform outline. By the time, however, that the ovules arise in the ovary and the bud attains a length of 1·5 mm., the eccentricity is definitely reversed and the posterior side is distinctly larger than the anterior, and this again becomes increasingly exaggerated in the older bud and flower.

type of *Selaginella*, in which the general form relations of the lateral members are indicated with a degree of accuracy quite sufficient to illustrate the main principles. It may be noted also that such a type, in which the leaf-members are not specialised to any extent, but remain in the primary " leaf-base " type of member, illustrate such simple mathematical construction relations much more obviously than is to be expected in more specialised petiolate forms in which the primary leaf-primordium may have undergone secondary segmentation. From the construction of the diagram it also follows that the greater the degree of eccentricity in the construction the more marked will be the anisophylly; so that in *Selaginella*, for example, the difference in the size of the two pairs of leaves becomes a measure of the amount of secondary divergence from the primitive radially symmetrical type.

That a shoot-system should become obviously eccentric in its growth and exhibit phenomena variously included under the terms " dorsiventrality," " zygomorphy," and " anisophylly," in the sense defined by both Wiesner and Goebel, is, however, after all not the most remarkable feature of such shoot construction ; or again that such eccentricity should be possibly induced by external environment, whether light action, as in the case of certain foliage-shoots, or as an adaptation to insect-visits, as in the case of many flower-shoots. The eccentric tendency may be inherent in any shoot, and especially so in lateral ones, and if at all advantageous may become exaggerated by natural selection with the production of its more or less marked after effects; but the most remarkable feature is not the existence of the eccentricity itself, so much as the manner in which the eccentric construction when markedly developed becomes established with a *constant orientation* in the phyllotaxis system. In other words, the displacement of the growth-centre in such cases is not accidental, but follows a definite direction which must often be accurate to a remarkable degree. These phenomena include both the *orientation* of the foliage of the " dorsiventral " shoot and the " *plane of zygomorphy* " of the eccentric flower-shoot. In the case of foliage-shoots, the production of an amount of structural eccentricity sufficient to appeal to the eye in the anisophylly of the leaves in the case of normal asymmetrical

phyllotaxis is very rare (*cf. Abies* sp.); and the fact that such a degree of "dorsiventrality" may be legitimately regarded as a secondary specialisation is suggested by the curious fact that in the great majority of such phyllotaxis systems the construction is symmetrical of the *distichous* $(1+1)$ type, the *decussate* $(2+2)$, and very rarely $(3+3)$ (*cf. Salvinia, Catalpa syringaefolia*); * thus giving, in the first case, two rows of leaves on the upper side of the shoot, and in the second case four lateral rows of the *Selaginella* type. But on comparing the orientation of such lateral shoots with the normal examples of distichous and decussate orientation, it will be noted that while in the former case the leaves may lie either in the transverse or median planes, and in the latter are cruciately orientated in these same planes, the assumption of eccentric development is accompanied by a displacement of the growth-centre in such a manner that the leaf-members are always left on the flanks of the now bilateral construction, and the growth-centre is displaced towards the upper side in such a way that distichy is replaced by two rows of leaves now apparently on the upper surface, and decussation by an accurate displacement at 45°, giving a diagonal orientation; while the $(3+3)$ system displaces at 30°, with the result that three anisophyllous rows are left on either flank. In fact, as opposed to the use of the term "dorsiventral," the more immediate purpose of the operation would really appear to be the *creation of a right and left side*, so that one would be as fully justified in calling a "dorsiventral" shoot *zygomorphic*, as a "zygomorphic" flower *dorsiventral* (*cf.* Goebel).

Such displacements have been variously described in terms of angular changes and "displacements," according as the general effect is judged by the eye; † but there can be little doubt that the same general construction principles continue to obtain, and that the scheme of fig. 97 conveys a very good summary of the facts of the case, the orthogonal intersection lines of the respective systems remaining unaffected. For example, it is clear that the greater the eccentric specialisation of a distichous shoot, the more nearly would the two rows of leaves appear as a single median line

* Goebel, *Organography*, p. 108.
† *Cf. Ibid.*, p. 112.

on the upper side of the shoot, and their anisophylly might tend to disappear.*

While, again, a marked degree of eccentricity is rarely met with in the case of asymmetrically constructed foliage-shoots, such a phenomenon is frequent in the case of spirally constructed flowers; and in such types the very general attempt to convert the floral diagram into a symmetrical circular expression has not only led to confusing results, but in many instances has served to conceal the essential asymmetry of the floral structure. Thus, in a typical Angiosperm flower the assumption of symmetry in the sporophyll region is so remarkable and so definite, that the circular plan of the floral diagram becomes the common convention, to which a quincuncial calyx or perianth as an outer investment appears almost as an accident of the construction; and when the asymmetrical region is thus limited to the members of a single contact-

---

* The case of *Salvinia* is of special interest: the embryo, as is well known, commences a normal asymmetrical development which is continued for three leaves constituting a single cycle. At the fourth node, symmetrical alternating whorls of three commence; that is to say, a $(2+3)$ primary system adds after one complete cycle around the axis a new path of distribution, the system thus immediately becoming symmetrical of the type $(3+3)$: less frequently $(2+2)$ symmetry is first attained at the third node (Pringsheim). Normal eccentricity is, however, superimposed on the construction, thus giving three rows of leaves on either flank. It is interesting to compare this architectural scheme for the position and even approximate primary shape of such leaf-members and the apparent order of development of these successive whorls with the ontogenetic or building account given by Pringsheim (*Gesammelte Abhandlungen*, vol. ii. p. 354), although so little of any scheme can be definitely checked at the actual algal-like apex. Thus, according to Pringsheim, the water-leaf arises first, and is followed by the foliage-leaf farthest removed from it, the other leaf on the same side as the submerged leaf last. The whorls then alternate in the same fashion. This agrees with the geometrical construction (fig. 97), but Pringsheim's theoretical schemes are based on a preconception of the importance of quadrant division in the segmenting cells behind the apex. Once it is admitted that the apical cell is not the ruler of the space-form, but an accident due to the special type of segmentation into relatively bulky cells, and that lateral members are not localised accurately to special segments, beyond the fact that regularity in production of cells and members must necessarily involve a certain coincidence between the two, the value of these segmental schemes is much diminished, and the drawings on which they are based do not afford any convincing evidence of their theoretical importance.

cycle the deviation from perfect radial symmetry may escape notice.

That many floral types, on the other hand, are asymmetrical throughout the whole sporophyll region, including the corolla, is undoubted; although, again, owing to the general tendency of the plant to promote efficiency in the floral mechanism by the reduction of the number of its parts, the number of members produced is often insufficient to give any spiral pattern to the eye. In such cases the Eichlerian convention of assuming circles as much as possible has been adopted: thus, while *Aconitum* cannot be regarded as anything else but asymmetrical throughout and slightly eccentric (perianth $(3+5)$, sporophylls $(8+13)$, growth-centre displaced anteriorly in the plane of sepal 2), many diverse views have been proposed with regard to the interpretation of the flower of *Tropaeolum majus.*

As in previous instances, a geometrical construction diagram may be readily prepared which will illustrate the phenomena to be expected in the development of an eccentrically growing asymmetrical construction. Thus, fig. 98 is drawn for an eccentric $(3+5)$ system, and fig. 99 for a $(5+8)$, in both of which, as in these zygomorphic flowers, the growth-centre has been displaced anteriorly owing to an increased rate of growth of the posterior side of the flower, and the plane of eccentricity follows that of the second sepal, which is not necessarily the median plane of the diagram, but sufficiently near it for practical purposes.

Consideration of fig. 99 at once shows important features; the curve construction, as before, is wholly built on orthogonally intersecting curves, and it follows from the mathematical properties of the numbers of the curves employed that the quasi-squares may be serially numbered. But the mathematical order of such enumeration is no longer that of increasing size; that is to say, *it is not the order of actually visible ontogeny*, although it still remains the theoretical order of the initiation of the growth-centres. In such a flower, therefore, some members would appear to arise as protuberances out of their normal spiral sequence, owing to the fact that those on the posterior side are growing at an increased rate, and those on the anterior side at a diminished rate.

It may further be shown by diagrams that by varying the amount
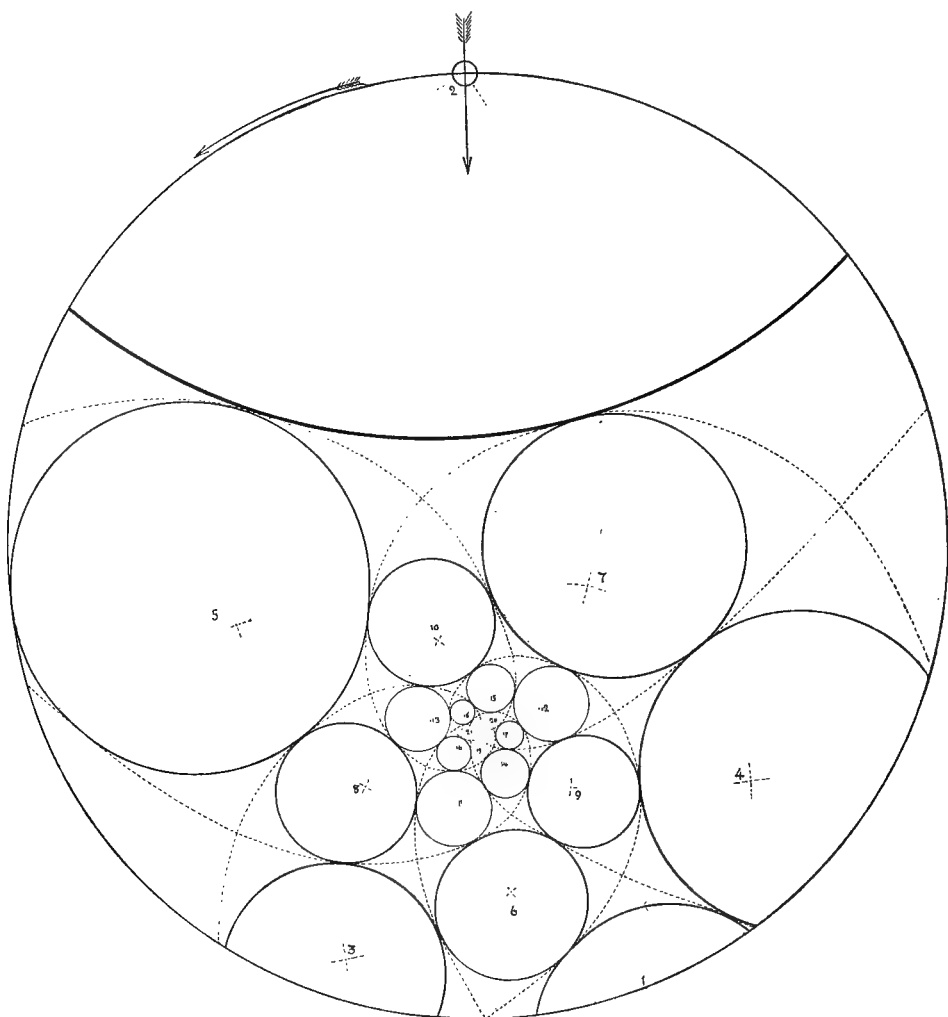
Fig. 98.—Eccentric growth, system (3 + 5) orientated for the plane of No. 2.
Growth-centre anterior. *Cf. Tropæolum majus.*

of eccentricity the details of such ontogeny would also vary, so
that no common rule could be given for the serial ontogeny of

floral types of varying degrees of eccentricity, while other complications occur, owing to the fact that eccentricity may not
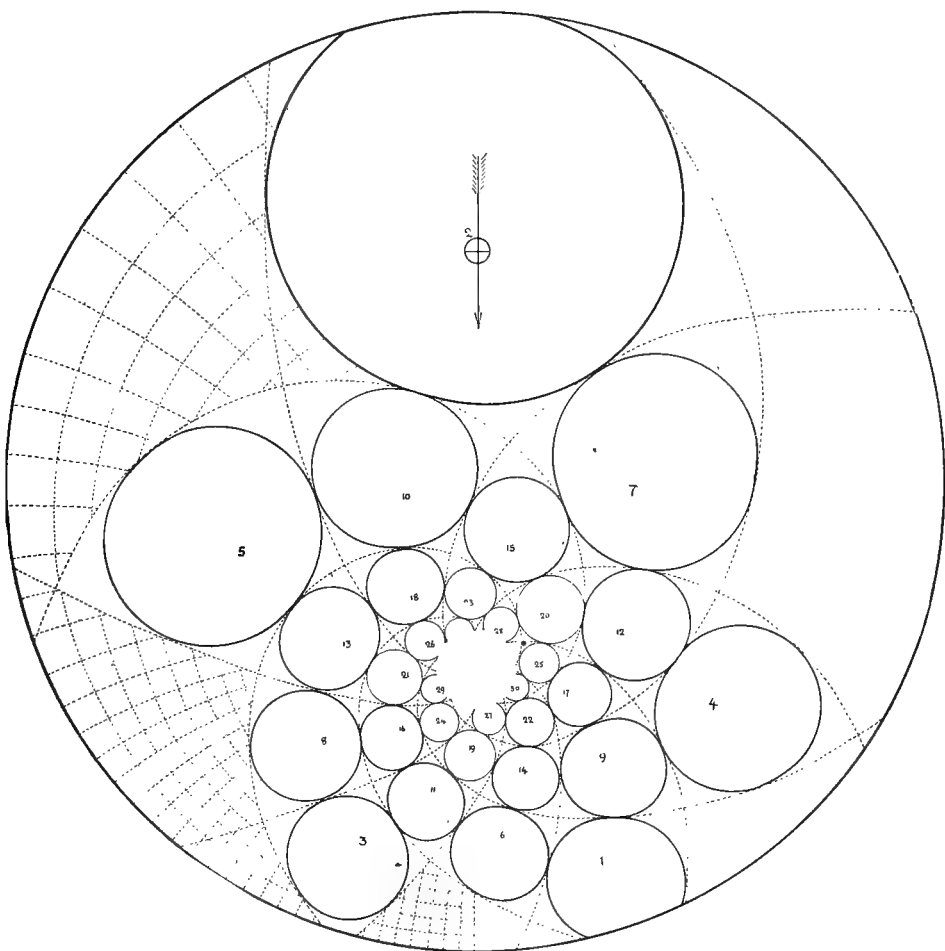

Fig. 99.—Eccentric growth-system (5 + 8), orientated for plane of No. 2. Growth-centre anterior ; a portion of the construction-network indicated on one side.

always follow the same plane of sepal 2. Every flower requires to be considered on its own merits, according to the time at which eccentric growth commences and the degree of eccentricity

attained. Thus, in fig. 99, eccentric in the plane of sepal 2, the increased rate of development of the posterior side of the flower involves the ontogenetic origin of members numbered according to their theoretical value to appear to the eye as if they had been produced in the sequence 2, 5, 7, 4, 10, 1, 3, 8, 12, etc. If, again, in the same figure, numbers 1–5 represent a normal quincuncial calyx, and 6–10 five spirally arranged succeeding petals, approximately alternating with them, 11–18 would be eight stamens and 19–21 three carpels, all in normal spiral series. Of these stamens, however, the apparently oldest would be 12, 13, 15 on the posterior side, 11, 18, and finally 14, 16, 17.

It now becomes of interest to compare the interpretations put forward to explain the construction of the flower of *Tropaeolum* (Freyhold, Buchenau, Eichler, Van Tieghem, Rohrbach, Celakovsky). The simple view which regards the androecium as consisting of two whorls of five, and the flower as cyclic, but with two median stamens suppressed (Van Tieghem, Eichler), affords no suggestion whatever as to the peculiar irregular ontogeny of the eight stamens. Nor can any attempt at manipulation of a "$\frac{3}{8}$ divergence," which would follow, according to Schimper and Braun, from the presence of eight members, account for the anomalous and yet fairly constant order of development, and more particularly for the postero-lateral position of the first to appear. Thus the sequence for a left-hand flower is:

$$
\begin{array}{c|cc}
8 & 4 & * \\
2 & 1 & \\
6 & 7 & \\
3 & 5 &
\end{array}
$$

According to the excellent account and figures of Rohrbach,[†] the position of 4, 5, 6 may vary somewhat. The calyx is admittedly spiral, but the axis is not apparently eccentric at this stage; the corolla is also spiral, as shown by Rohrbach; the second petal being distinctly larger than the others at first, shows that eccentricity now sets in. The fact that the stamens arise singly in an irregular order, and not strictly "ascending" or "descending," implies that whorled symmetry is out of the question and that

[*] Eichler, *Bluthendiagramme*, ii. p. 298.　　　[†] *Bot. Zeit.*, 1869, p. 848.

spiral construction must be involved. Since the members are few and the calyx apparently normal $(3+5)$, there appears little reason to doubt that *Tropaeolum* is a spiral $(3+5)$ type throughout all its parts, retaining 5 sepals, 5 petals, 8 stamens, and usually 3 carpels (less frequently 4–5) in normal spiral sequence, which is, however, affected in so far as the numerical order of apparent development is concerned by a pronounced degree of eccentricity.

Thus, according to the diagrams, figs. 98, 99 show that the amount of eccentricity of the developing flower lies between these two figures ; the former shows eccentricity proceeding at a greater rate, while in the latter it has affected a greater range of members. The agreement of fig. 98 with the data of Eichler and Rohrbach is not only very close, but it conveys in itself the reason why the data may slightly vary (Rohrbach, *Bot. Zeit.*, 1869, p. 848, figs. 1, 5 16, 17); while observation of the error of the geometrical construction shows the difficulty of accurately gauging the relative size of the primordia by the eye, the error of the geometrical method being again less than that of observation of the protuberances on the actual shoot apex. Thus in fig. 98 the sequence of apparent origin would be considered to be 12, 11, 13, 14, 15, 16, 17, 18 ; or

$$\begin{array}{c|c} 8 & 5 \\ 3 & 1 \\ 6 & 7 \\ 2 & 4 \end{array}$$

while in fig. 99 it would be 12, 13, 15, 11, 14, 18, 16, 17 ; or

$$\begin{array}{c|c} 6 & 3 \\ 2 & 1 \\ 7 & 8 \\ 4 & 5 \end{array}$$

It is clear that if the eccentricity of the former diagram had proceeded further 13 would have become larger than 11, that is, 3 would have replaced 2 in the first scheme ; while if the eccentricity of the latter had not been carried so far 15 would not have appeared larger than 11 and 18 would not have been larger than 16 and 17, these being the changes required to bring either scheme into agreement with that of Rohrbach.

There can be little doubt that the explanation of the *Tropaeolum* flower is remarkably simple, once the effect of an unequal rate of growth on one side of the whole shoot and its appendages is understood, and that such construction diagrams not only include between them the facts of observation, but point out the degree to which variation may be expected, according to the amount of eccentricity obtaining at the moment of observation.

The flower of *Tropaeolum majus* is thus in all probability a (3 + 5) asymmetrical type throughout; its eccentricity being still further complicated by : (1) the delayed development of the corolla, so frequent in petaloid types, these members being greatly retarded at first, so that the relation of the corolla cycle to the spiral sequence is not apparent; (2) the stamens also present a degree of growth retardation which causes them to lose at an early date the normal contact-relations of a (3 + 5) system, and so loosen out until the contact-relations of the next type (5 + 8) are approximated (fig. 99), in which eight members are required to fill a contact-cycle. A ninth stamen, if produced (No. 19), would be median anterior, and the orientation of the carpels slightly oblique.

As opposed to the Eichlerian type of diagram, a convention based on the visible structure of the bud, these schemes become structural diagrams for the primary distribution of growth-energy in the initiation of the floral members. An attempt has been made in fig. 99 to approximate the amount of eccentricity required to agree with known data, if the system had retained uniform growth in all its parts; the fact that the flower illustrated is " left-hand " resulting from the direction in which the fundamental construction curves cross one another (fig. 34).

Given these fundamental phyllotaxis phenomena as the basis of the construction of the flowering axis, it now becomes possible to isolate all superimposed variations and alterations in the relative rates of growth which collectively determine the formation of a *floral mechanism* from a mere collection of uniform lateral appendages.

V. The Bilaterality of Appendages.

SINCE it follows from the mathematical construction of a circular system of lateral members, making close contact and exhibiting uniform growth expansion, that no absolutely radially symmetrical member can be primarily produced from the growth-centre and remain a part of the system, a comprehensive definition of a foliar member is thus obtained, in that all leaf-structures must be by construction *inherently bilateral* from their first inception; and although the true curve of the transverse section of a member may differ from a circle only within the error of drawing, these primordia are always eccentric with regard to the point which has been termed the "centre of construction."

The biological observation that "stems" bear "leaves" in acropetal series is thus correlated with the mathematical fact that such inherently bilateral primordia can alone be primarily produced by a growing apex so as to satisfy the observed phenomena. Radially symmetrical "branches," on the other hand, are to be regarded as secondary productions, and arise at a greater distance behind the growing-point; as, for example, in the apparent axil of a previously formed primary primordium, these areas being the only spots left vacant in a normal growing system.

Every leaf, or lateral member of the first degree, whether borne on the axis of gametophyte or sporophyte, whether an assimilatory appendage or a sporophyll, is thus structurally bilateral from the first; and however much certain types may subsequently become "centric" in form, they remain nevertheless eccentric internally, with regard to the centre of construction, so long as any growth

persists; although, again, the amount of eccentricity may be very slight, and, when the bulk-ratio is small, quite inappreciable to the eye. In the case of sporophylls, more especially stamens, the approximation to a circular section in the developing primordium may be very close; * but in the majority of foliar members the structural bilaterality becomes increasingly exaggerated in the form of the so-called *dorsiventrality* of the leaf, as these members become specialised as assimilating laminae, exposing the maximum surface to gaseous interchange.

In fact, the primordia seen at the apex of a typical leafy shoot are usually obviously bilateral from their first appearance, and thus apparently flattened in a tangential direction; but as previously indicated, their first appearance tells little of their first inception. And, just as it has been shown that a uniform cessation of growth at a certain stage in all the lateral members may, as in the case of *Coleochaete* (fig. 87), suggest the appearance of a uniform growth-increment comparable to the effect of a uniform growth-movement expressed as a uniform velocity; or again by the subsequent attainment of a constant bulk in the lateral members may create a subjective impression of torsion-spirals, intersecting as helices on a cylindrical axis where no torsion exists; so this flattening of the members will necessarily produce appearances to a certain extent suggestive of the action of a strong compressing force. There is no need whatever to assume that the first production of bilateral symmetry in a leaf-primordium is caused by the stimulus of any mechanical pressure in the bud; it depends primarily on the actual mechanical construction of the growing zone. The primordia which subsequently grow according to their inherent dispositions are able at first to resist all pressures of adjacent primordia; and so long as these are equally distributed along orthogonal paths of construction, the

* An interesting example is afforded by the development of the sporophylls of *Clematis* (*C. integrifolia, Jackmanni,* etc.), and a comparison with the formation of the primary branches of the terminal umbel of such a form as *Heracleum giganteum*. The former presents a system of leaf-members, the latter a system of branches whose subtending bracts are suppressed; but to the eye the appearances presented by the two cases, and the shape of the primordia and their contact-relations, are identical so far as can be judged.

greatest mutual pressures can only press them into close rhomboidal contact and convert their section into the form of quasi-squares.

The appearance presented by a typical foliage-bud, however, is very different from any such theoretical construction; and it is clear that the assumption of the considerable amount of flattening included under the conventional use of the term "dorsiventrality," which is much greater than that of the original primordium, must entail correlated alterations in the rates of growth. The secondary flattening of the member is most simply regarded as the effect of a diminution in the rate of radial growth of the whole system (fig. 100); and as soon as the members diminish in radial growth at a greater rate than the axis does, the bud loosens its contacts and begins to open out. Such diminution of radial growth may also produce the effect of a tangential extension where this does not really exist, or again it might be associated with such an increased tangential rate of growth. The several cases may thus be considered from the standpoint of differences in the rates of growth-expansion in two directions, the radial and the tangential, these being represented in any given system by the diagonals of the rhomboid meshes, which in the case of spiral systems are both spiral lines.

In a typical bud, again, this "flattening" is also always associated in spiral systems with a phenomenon of "sliding-growth," which is one of the most remarkable properties of a leafy shoot, in that the method adopted is perfectly definite. The leaf-members exhibit a certain amount of slipping at their edges, and the arrangement is carried out with the greatest precision, so long as the construction is asymmetrical and spiral. It must be noted, however, that the corresponding phenomena in the case of whorled symmetrical constructions is either wanting (*cf. valvate* prefloration), wholly irregular, or very rarely according to a definite scheme (*cf.* convolute prefloration). In fact, it appears possible even at this point to make the generalisation that a certain primary sliding-growth must be a mathematical necessity of *assymmetrical* construction in phyllotaxis systems.*

* Cf. Mathematical Notes.

In dealing with such a phenomenon it is necessary, to begin with, to distinguish between facts of observation and any inter-
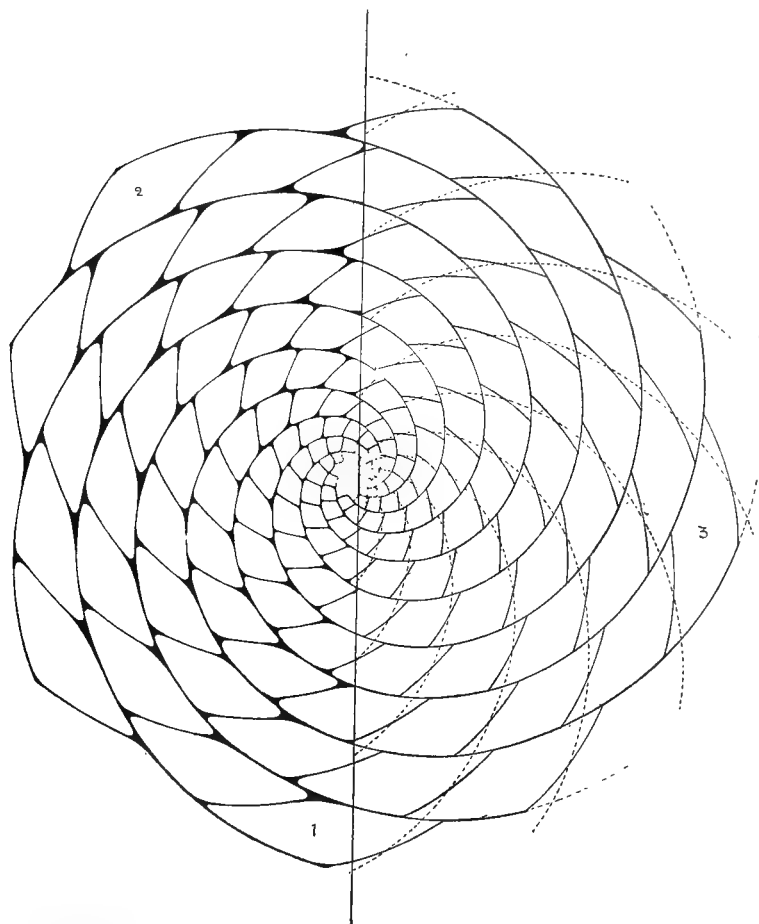
Fig. 100.—Geometrical construction, including progressive "dorsiventrality" and sliding-growth effect for system (8+13). Drawn with construction curve (Type II.) for uniformly retarded growth.

pretations which may have been ascribed to them. Now the facts observable are very definite: the rhomboidal primordia apparently thrust laterally along their tangential diagonal, and as

Fig. 101.—*Campanula medium*, L.   Perennating rosette, system (5 + 8).

they thus appear to become tangentially elongated a certain
amount of slipping takes place at the angles. Such sliding-growth

Fig. 43.—*Sedum elegans*ᵤ̈(6 + 10).

is most simply described as comprising a *stepping of the shorter
construction curves*, while the longer ones remain unaffected and

U

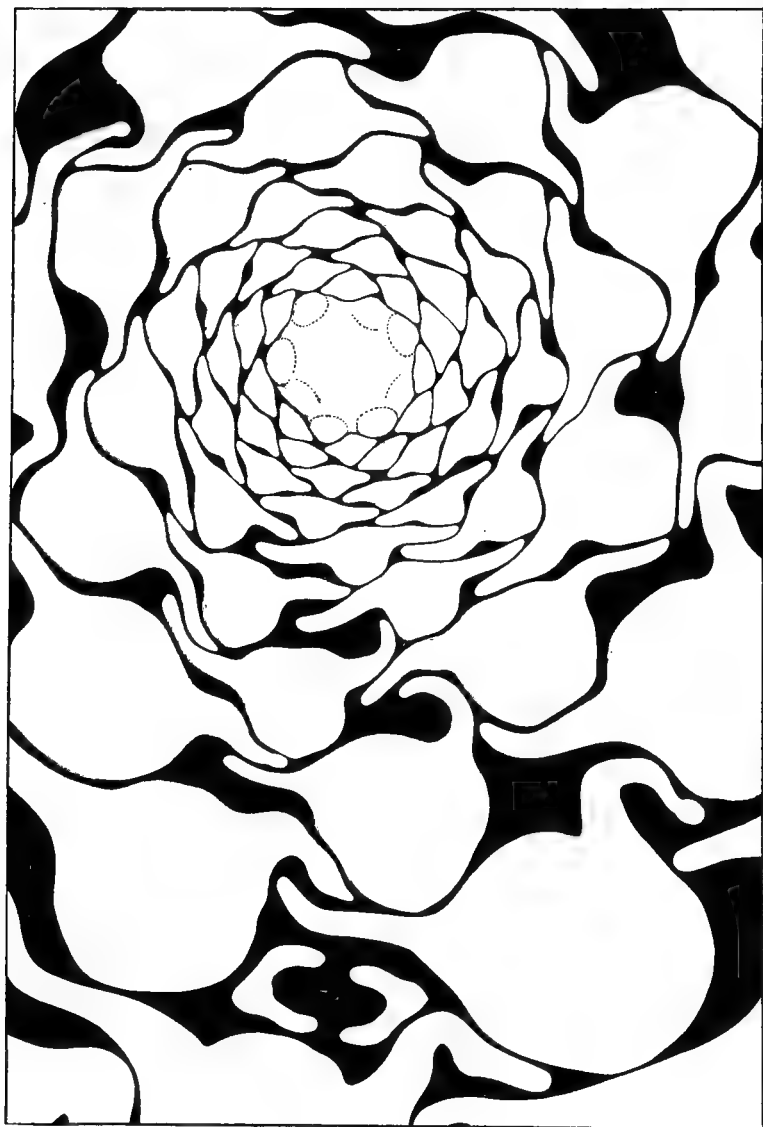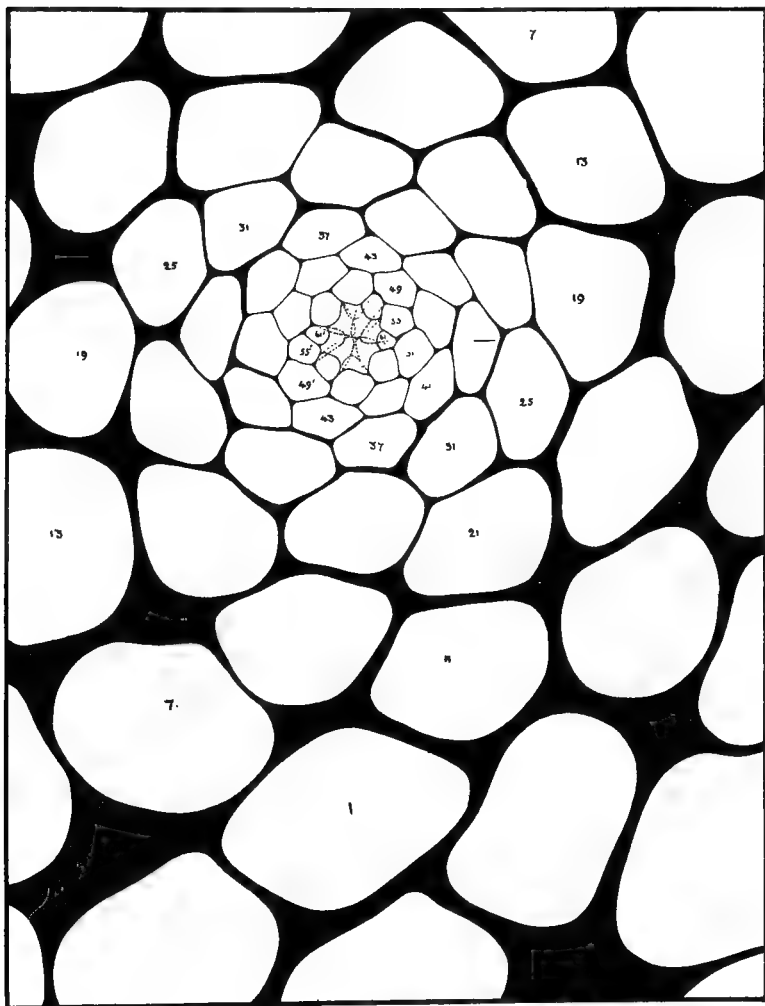are thus rendered increasingly obvious; so much so, that when the sliding effect is considerable they can alone be readily checked. From this standpoint it is easy to introduce the phenomena of normal sliding-growth into the construction diagram, as in fig. 110 $(5+8)$, or again as in the $(8+13)$ system of fig. 100, in which the
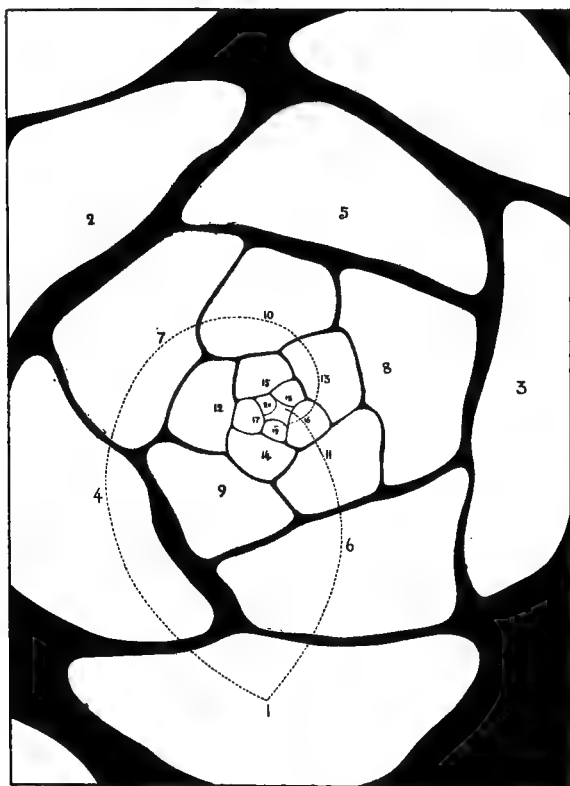
Fig. 102.—*Sedum acre*, L.   Perennating bud, system $(3+5)$.

scheme consists of a normal phyllotaxis system plotted, however, with a curve of the second type,—of *uniformly retarded growth*, —which conveys the information that a progressive retardation in the radial rate of growth of the system as a whole produces the effect of a progressive "dorsiventrality" in the leaf-members. But while the progressive increase of dorsiventrality in the

members is thus associated with a certain amount of sliding-growth, it does not follow that the two phenomena are in any way dependent one on the other; the progressive flattening may be clearly ascribed to a reduction in the rate of radial growth, which is common to symmetrical as well as asymmetrical constructions, and must obtain in the transverse component of all dome-shaped apices; the sliding effect may be entirely isolated from such a retardation effect, just as in the diagram the reduction in the rate of radial growth-expansion can be imitated by using a curve expressing this factor, but the sliding effect has to be put in subsequently.

It becomes apparent that the consideration of the phenomena thus included under the general term "sliding-growth," in connection with lateral appendages, requires very careful handling, in that it might evidently be the result of several distinct growth-factors; and as in other cases, the first-suggested interpretations may not be the right ones. In fact, the true interpretation of such lateral slipping is of great importance, since it constitutes the most important evidence in connection with Schwendener's displacement theory: the Dachstuhl theory assumed that flattening implied a pressure, and that such readjustment of the angles of the primordia indicated a *displacement* of the whole member, and thus affected the divergence-angle and thereby altered the postulated Schimper-Braun construction. The diagrams (figs. 100, 110) sufficiently indicate that no amount of such sliding-growth really affects the primary construction system which is taken from the initial points, *i.e.* the centres of construction, while, as has been already repeatedly stated, mere flattening is only the expression of reduced radial growth.

In considering the meaning of these phenomena it may be pointed out, to begin with, that the displacement of the points of contact of four boundary planes does not necessarily involve any displacement of the original centres of construction; this, in fact, is the usual result of the effect of lateral contact-pressures, comparable with the special case of fitting previously indicated as giving to an otherwise orthogonal construction the appearance of hexagonal facetting (fig. 95, Pine-cone), or the typical adjustment

of the radially elongated ovaries of *Helianthus.* Even in the case
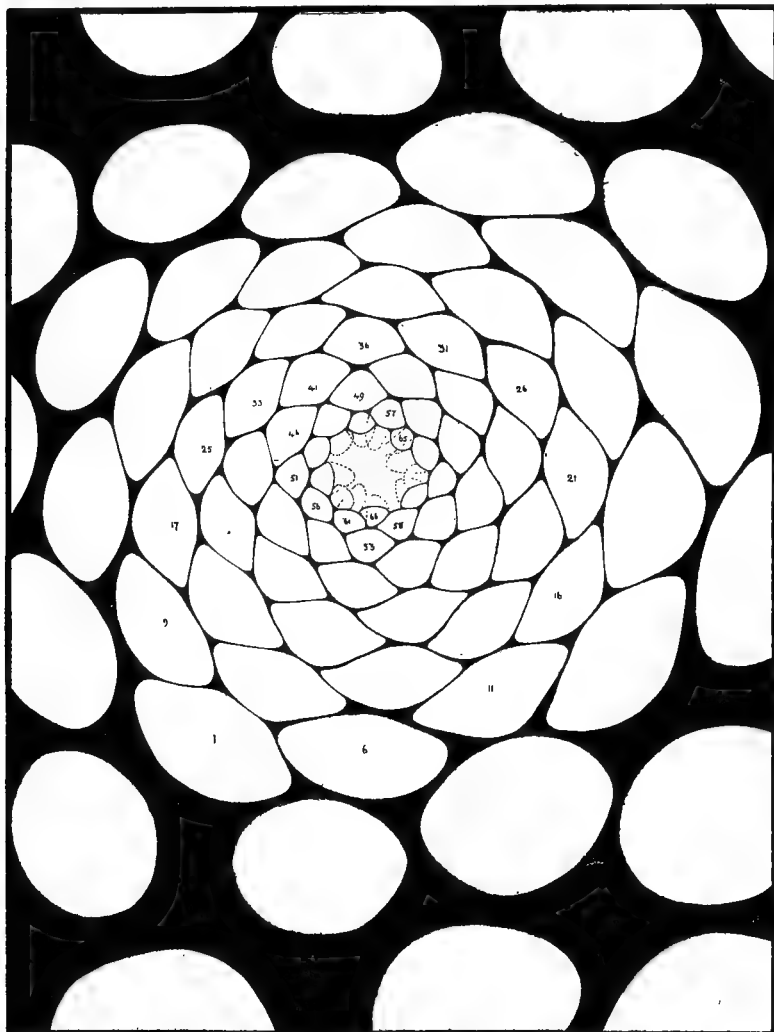of four cell-walls meeting at right-angles, such slipping normally

Fig. 103.—*Sedum pruinatum*, Brot. Leafy shoot, system (5+8).

obtains, and is always allowed for in a tissue-drawing,—the four
cell-walls at 90° tending to pull into two sets of three: this

appearance has been noted by Sachs as a secondary phenomenon presenting no real objection to the primary construction of tissue masses by orthogonal trajectory curves (*cf.* Sachs, *Physiology*, p. 433). Thus a slight displacement in a primary orthogonal $(5+8)$ system has little effect in altering the construction as a whole, and the diagram closely represents the fact observed in a section of the adult stem-apex of *Nymphaea* (fig. 110).

Secondly, the existence of similar slipping in the form of a growth adjustment has already been shown to occur in connection with the arrangement of lateral axes which have only a subsidiary connection with the primary system of foliar appendages. Thus, in the stock examples of the *Helianthus* capitulum, the Pine-cone, and the Aroid spadix, it was evident that any secondary extension of a member which was not a foliar appendage, either radially or tangentially, must produce a similar sliding effect; the "stepping" affecting different curves according to the geometrical necessities of the construction. That is to say, any variation in the bulk of a lateral appendage at a point beyond its insertion will produce alterations in the system if section takes the members at this point; and it must be remembered that the transverse section of a typical bud with dome-shaped apex cuts the peripheral members at a higher level of their course than in the case of the youngest primordia. Further, a tendency of a leaf-primordium to become wider tangentially in some part of its course, above its insertion, may also be taken as typical for the great majority of foliage-buds. Any such increased tangential growth of a primordium at a point above its base, while these insertion-areas still constitute the surface of the axis, must necessarily involve a readjustment slipping of the same type as that found in the scales of the Pine-cone; that is to say, the short curves will become stepped. Variations in the bulk of the appendage at different parts of its length will thus produce sliding effects in both asymmetrical and symmetrical systems: in the former the sliding will follow the tangential diagonals in an orderly manner, since the paths of such sliding are left obvious in the construction; but in the case of symmetry the overlapping will be quite irregular, since normally the primordia should accurately meet at their

edges (*cf.* valvate prefloration), and there is no reason why the slip should take place in one way more than the other.
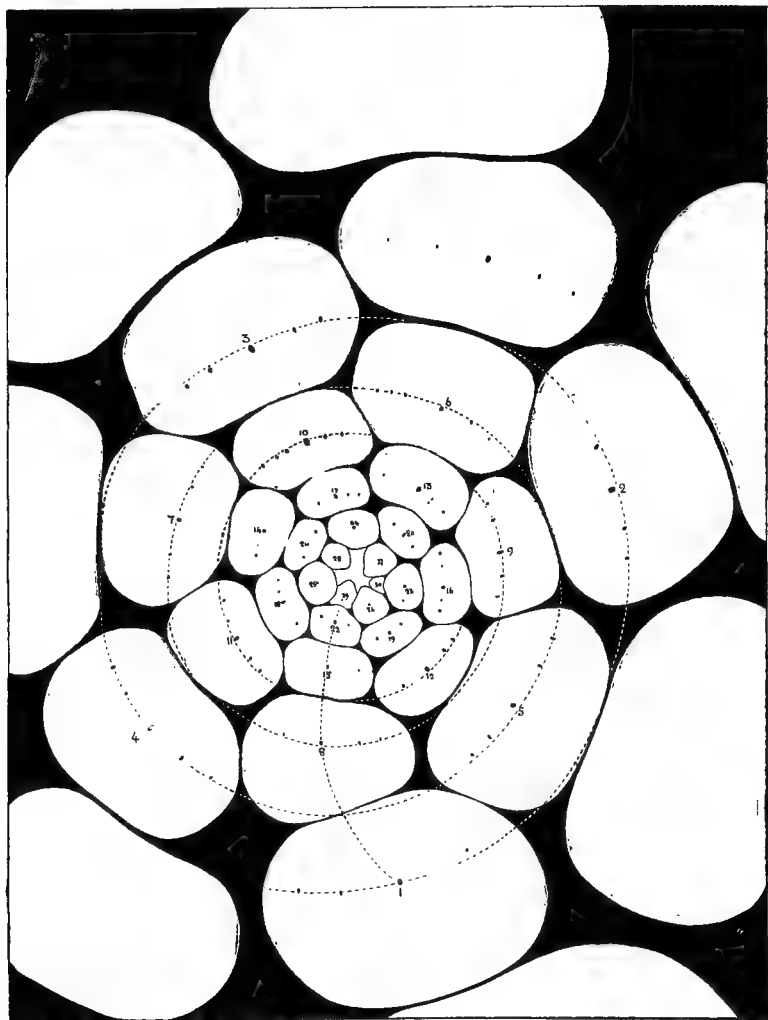

Fig. 104.—*Sedum reflexum*, L. Perennating shoot, system (3+4)=7-spired: the vascular bundles follow the spiral of dorsiventrality, which is here also the ontogenetic spiral.

$$\frac{2}{7}$$

But even these effects are only of secondary importance, since it is clear that any change in the *volume* of the lateral appendage beyond the area of its insertion can have no reference whatever to the primary construction of the system, although it may tend to produce all the normal appearances of sliding-growth. Much less, therefore, can similar effects, produced by changes in the volume of axillary shoots, etc., as in the case of the Pine-cone, and aggregated inflorescences (*Helianthus*), have any bearing whatever on the subject: such changes can only be included as *tertiary* factors; and one wonders more and more at the curious standpoint which has sought to find in these tertiary effects a basis for the Dachstuhl theory. On the other hand, the possibility still remains that in the theoretical and mathematical construction of asymmetrical phyllotaxis systems there may still exist a *primary* cause for these displacement movements; and as a matter of fact, the necessity for such readjustment of the free portion of the appendage follows directly from the mathematical consideration of the log. spiral theory.*

The discussion of this readjustment, which implies a slight rotation of the primordia about their centres of construction, and is also only applicable to cases of asymmetrical construction, may therefore be postponed until the equation to the quasi-circle primordium has been deduced: at present it will be sufficient to consider the geometrical consequences of adding the compensation for such " sliding-growth " to the theoretical diagrams.

The spiral construction diagrams, as expressed by intersecting curves giving rhomboid meshes, present a good working idea of a typical foliage-bud in which the members have, in consequence of mutual growth-pressures, filled all the room available to each primordium, and thus assume an obliquely rhomboidal section (*cf. Pinus*, fig. 88; *Araucaria*, fig. 41). A section of such a bud at the level of the growing-point includes the insertion-areas of the members close to the apex; but away from this the members will be cut at some distance above their bases, owing to the character of the dome-shaped apex. The plane diagram, therefore, represents insertion-areas only, and these alone are now under

* *Cf. Mathematical Notes.*

consideration; that is to say, these figures include the study of the relationships of adjacent *leaf-bases*.

Observation shows that, as the rhombs are progressively extended along their transverse diagonal, the shorter construction curves are "stepped"; and since these diagonal paths were also originally log. spirals, the curve of a value one stage lower in the summation series than the numbers expressing the ratio of the curves composing the system (*i.e.* their difference) may be conventionally termed the "*Spiral of Dorsiventrality*." From this standpoint a bifacial leaf is only flattened in a strictly horizontal plane when it is produced in a *symmetrical* phyllotaxis system; in which case the paths of lateral extension are concentric circles: in the more general case of *asymmetry*, structural dorsiventrality becomes exaggerated along a spiral path, which has therefore no *direct* relation to external environment, as, for example, the action of vertical light, although it is the nearest approach possible to a horizontal line in each rhomb. In other words, the architectural scheme of each shoot is controlled by the growth-centre of the axis, which is the fundamental growth-centre of the whole shoot-system, and here, as in the case of eccentricity, the influence of external environment, if this is the determining agent, must act on the primary centre at the end of the shoot, and all subsequent architectural details are worked out according to strict geometrical principles. These construction diagrams further show that the result of the sliding-growth effect is here to place this tangential diagonal more and more in a horizontal line : a teleologist might at this point even make the suggestion that the object of the sliding effect was of the nature of a biological " adaptation " which would render the surface of the leaf-lamina more strictly horizontal; but such an explanation is wholly gratuitous. The distinction which is here drawn between the geometrical plan of leaf-base insertions and the geometrical properties of the free portions of the primordia, as expressed in the lamina portion of the leaf, will be further discussed from the standpoint of the mathematical equations of the theoretical curves (*cf. Mathematical Notes*, VIII.).

A few interesting details are also more clearly exhibited by

such theoretical diagrams; thus, as each leaf-rhomb is extended laterally, over an older primordium and under a younger member, the shorter curves assume their characteristic serrated appearance, and the long curves remain with an unaltered clean contact edge. The recognition of the phyllotaxis ratio of such a growing shoot then becomes increasingly obvious; the smooth edges of the lines of contact of one set of curves directly indicating that they must be the longer curves of the construction.

Again, the lower the parastichy ratio in the Fibonacci or any other series, the more marked is the "spiral of dorsiventrality" as an obliquely horizontal path; while with higher ratios this so nearly approaches a circle that the flattening and position of the leaf-insertions along a spiral path are not readily observed; nor will it be noticed when dorsiventrality becomes excessive, or again is correlated with phenomena of sliding growth.

Thus, in the case of the sporophylls of *Stangeria* (fig. 29), the rhombs are obviously extended along an obliquely horizontal spiral, and the same fact may be noticed in Pine-cones; while in the lowest cases of asymmetrical phyllotaxis, the oblique insertion of the members becomes very marked (*cf. Gasteria*, fig. 58*a*). Also, comparison of the diagram (fig. 110) shows how little the amount of sliding may be that is sufficient to bring the transverse diagonal of each rhomb very approximately parallel with the circle, *i.e.* truly horizontal.

It is also obvious that the "spiral of dorsiventrality" does not bear any necessary relation to the "ontogenetic spiral" in a given shoot: it is the spiral which is orthogonal to the curve previously termed Schimper's orthostichy line, and since this latter, which bisects the angle of the intersection of the construction spirals, winds in the direction of the longer curves, the "spiral of dorsiventrality" always follows the direction of the shorter spirals, and bears the same relation to the genetic-spiral as do these (*cf.* Table, fig. 34). With a right-hand genetic-spiral, that is to say, the foliage-leaves on a $(2+3)$ and a $(3+5)$ shoot are obliquely inserted in converse directions, and their bases remain obliquely inserted even after the shoot has passed through a zone of elongation which renders Schimper's orthostichy line sufficiently straight

to the eye, this being especially well seen in the case of leaf-scars.

Similarly, the exaggeration of the primary bilaterality of a primordium may follow the path of the so-called orthostichy spiral, which intersects the spiral of dorsiventrality orthogonally.
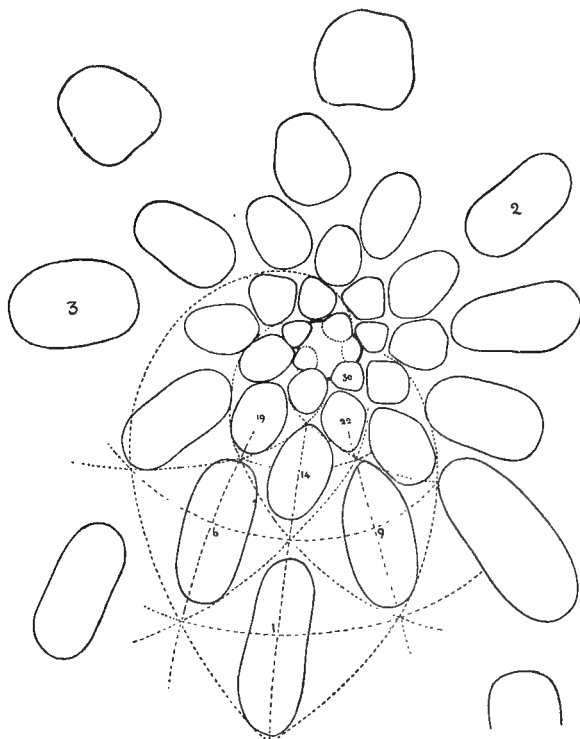
Fig. 105.—*Acacia cultriformis.* Young shoot of phyllodes, system (5 + 8).

The insertion of *phyllodes* and "isobilateral" members in packed asymmetrical phyllotaxis constructions does not necessarily follow an exactly vertical plane corresponding to any direct stimulus of vertical light, but follows the path of the spiral diagonal, which is very nearly vertical. The spiral path becomes more approximately radial (vertical) as the phyllotaxis ratios approach equality, but in Fibonacci systems the spiral nature of the path is obvious

in the diagram: thus in young growing shoots of Phyllodinous Acacias (fig. 105) the development of the phyllode lamina along slightly spiral vanes (spires) is readily recognisable; and the same generalisation holds for the secondary protuberances which constitute the ridges of the Cactaceae (*spiral of phyllody*).

On the other hand, with the assumption of the special case of true symmetrical construction, these geometrical relationships vanish, in that the complementary diagonals of the quasi-squares become circles and radii respectively; so that in a whorled type the leaf-laminae lie in a strictly horizontal plane from the first, and a whorled phyllode is also wholly orientated in a vertical plane.

Finally, it may again be noted that all these generalisations, being applicable to the rhomboidal section of a leaf-primordium presented in a phyllotaxis system in which the leaves tend to take the form of quasi-squares under mutual pressure, do not directly concern the relationships of the free primordia of the primary system. The nature and symmetrical properties of the primary primordia, which in section present the form of an ovoid curve, which in the theoretical construction is to be regarded as a quasi-circle, require to be considered separately, when the mathematical properties of such constructions have been more fully described (*cf. Mathematical Notes*); the special point, of interest being that, while in asymmetrical constructions the rhomboid sections are also asymmetrical and obliquely placed, the fundamental curve of the primordium is mathematically orientated from the first along a radius of the whole system passing through its centre of construction, and about which radius the member is truly bilaterally symmetrical.

A clear distinction is thus required to be drawn between the behaviour of the leaf-base, as seen at the insertion-area (or leaf-scar), which is the surface of the axis, and the properties of the free portion of the lateral appendage.

As general examples of these various phenomena, comparison may be made of the sections of the terminal buds of *Pinus* (fig. 88) and *Araucaria* (fig. 41), in which the amount of sliding-growth is relatively small. The transition is shown very perfectly

in *Podocarpus* (fig. 42) and *Euphorbia Wulfenii* (fig. 90), in which a very considerable degree of "dorsiventrality," accompanied
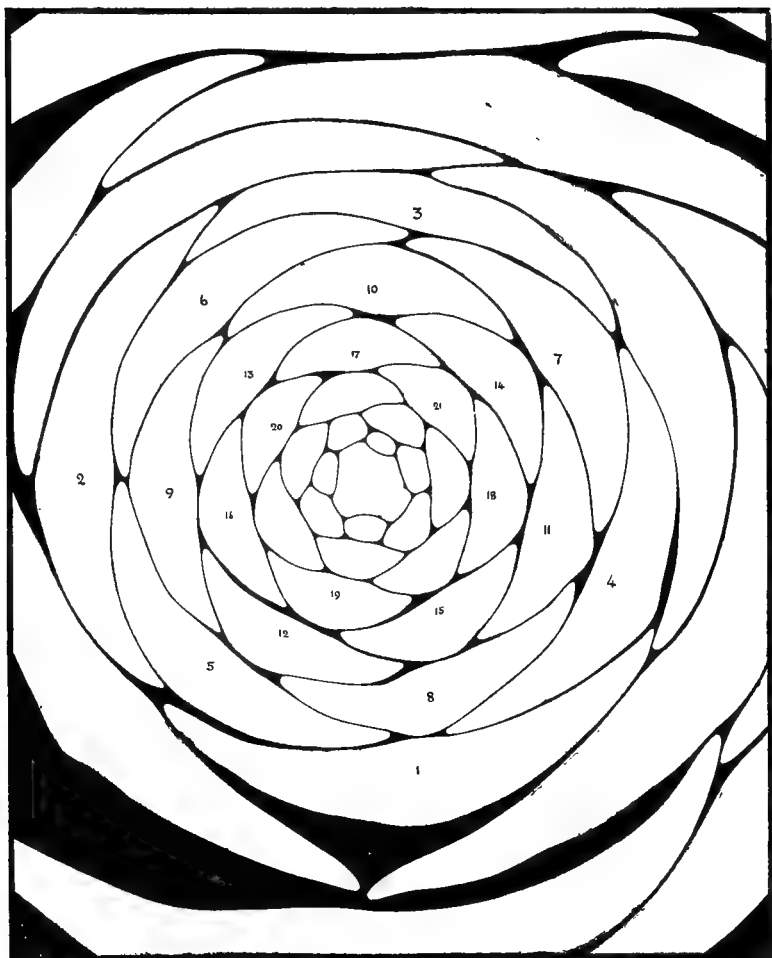

Fig. 106.—*Euphorbia biglandulosa.* Spring shoot, system (3 + 4).

by a well-marked sliding readjustment, is attained at a short distance from the apex. Species of *Sedum* with so-called *centric* leaves present a point of interest in that, while the primordia are

at first approximately isodiametric, "dorsiventrality" at first proceeds normally, and the leaves only attain their adult pseudocircular outline at a later date (*cf. Sedum pruinatum* (5 + 8), fig. 103; *S. elegans* (6 + 10), fig. 43; *S. reflexum* (3 + 4), fig. 140). The "spiral of phyllody" is clearly indicated in spring shoots of *Acacia cultriformis* (fig. 105), though rapid elongation in the main axis tends to prevent the full effect from being observed in a section passing exactly transverse to the growing-point: the diagram illustrates a section cut slightly obliquely on one side.

It will also be noted that, just as "dorsiventrality" becomes normally associated with a "stepping" of the shorter curves, so phyllody must similarly be connected with a stepping of the long curves, the phenomenon being identical with that previously described for the disk-florets of *Helianthus* (fig. 89).

GEOMETRICAL REPRESENTATION OF BILATERALITY.

Owing to the extreme development of bilaterality in typical foliage-members, the number of leaves seen in a transverse section of a bud is usually so greatly increased that the primary log. spiral construction curves are clearly wholly inadequate for the expression of the modified construction (fig. 3). At the same time, as the members enlarge with a diminishing rate of radial growth, the curves cease to be log. spirals, and when growth ceases, and all the members have attained an approximately uniform bulk, the construction lines necessarily pass into curves which cannot be readily distinguished by the eye from spirals of Archimedes with equidistant coils, and in the theoretical case would be such curves (*cf.* fig. 4).

A construction by definite spirals of Archimedes in the suitable ratio thus presents to the eye a system much more in accord with what is actually seen over the greater part of the area of a section of a foliage-bud than that of the primary hypothetical log. spirals, owing to the fact that the rhombs plotted by the parastichy curves may have very nearly equal radial depth. The appearance of progressive "dorsiventrality," as the rhombs become relatively

flatter and flatter at the periphery of the system, is also very nearly approximated; while it is clear that such Archimedean spirals would be replaced by helices on a cylindrical axis, and thus constitute the ultimate spirals observed on the adult plant, in which growth may be considered to have wholly ceased. A curve-tracing for the expression of these secondary growth-phenomena may thus be constructed by taking the central portion as normally log. spiral, while at the periphery the curves grade into the corresponding spirals of Archimedes. With such an empirically constructed curve-pattern a system of dorsiventral primordia may be plotted, which, when due allowance is made for the phenomena of sliding-growth adjustments along the spiral of "dorsiventrality," presents a most accurate imitation of the phenomena observed in the macroscopic view of a plant which presents only these modifications of its construction system in the adult condition (*cf. Sempervivum spinulosum*, fig. 4).

On the other hand, it is equally clear that, so long as any *growth* persists, the curves will never really become spirals of Archimedes, although the approximation may be very close to the eye, and the previous construction will not correctly interpret the phenomena observed in the section of a growing apical system, as seen, for example, in a transverse section of the apex of *Euphorbia Wulfenii* (fig. 90) or *Podocarpus japonica* (fig. 42) which comprises young growing members only. Since "dorsiventrality" may be regarded as the expression of a decrease in the radial growth of the primordia, the log. spiral construction curve may be modified by giving it a radial retardation; and for present purposes it may be sufficient to assume that such retardation may be uniform. A curve of this form (Type II.) may therefore be used to plot a system which is still growing, but at a progressively slower rate (fig. 100), and by adding the sliding adjustment which steps the shorter curves, a very close approximation is afforded to the *Euphorbia* section of fig 90— at any rate, one so close that the amount of error is not appreciable to the eye, the actual rate of retardation not being known.*

* Thus, fig. 100 represents a simple geometrical construction in which uniform growth at the hypothetical growth-centre undergoes subsequently

Extreme " dorsiventrality."—As the lateral extension of members becomes excessive, and their radial depth as seen in transverse section more and more approximately uniform, it is clear that a construction by spirals of Archimedes, which give on intersection rhombs which are extremely flattened out in a tangential direction, will closely simulate all observed phenomena, so far as the eye can judge, although they may never be absolutely correct for growing systems. Thus, by constructing such diagrams ((2+3), fig. 107; (3+5), fig. 109) using a pair of Archimedean spirals (fig. 33) continued to the second and third intersection respectively, the structure of "dorsiventral" leaves of the extreme form found in foliage-buds is very closely *imitated*, and by adding the theoretical slipping across the paths of the shorter curves, it will be seen that all the phenomena observed are fairly accurately planned. Good results are thus obtained for floral diagrams of adult flowers, although for buds better ones would result from a retardation curve. At the same time it must be noted that Schimper-Braun constructions are being utilised, in which the structural error now becomes too small to be noticed.

Nothing is more remarkable in dealing with the sections of a large number of buds, than the extent to which growth is normally so correlated in the whole shoot-system, and the amount of lateral sliding remains so fairly constant in the section that the

a uniform retardation, with a consequent alteration of the curve-system. It must be remembered that uniform growth remains a purely mathematical conception, and the log. spirals drawn to express it may be distinguished as curves of the *First Type*. Similarly, the assumption of a uniform retardation is equally a mathematical conception, which, though it may represent a nearer approximation to the truth, evidently does not yet contain the whole truth, since, whatever such a retarded growth may be theoretically, a general knowledge of growth-processes in living organisms suggests at once that such protoplasmic growth would show daily and even hourly variations on the curve the more accurately it could be plotted. These considerations, however, will not prejudice the attempt to reach a solution of the phenomena by mathematical conceptions, so far as it may be possible : they serve to indicate that the conditions become more and more complicated, and the simpler hypotheses require to be taken first. Assuming a uniform retardation as a secondary conception, the curves which are used to plot such a construction may be distinguished as curves of the *Second Type*.

original contact-relations may remain largely unaffected, and the recognition of the phyllotaxis constant for any given bud may be rendered easy, however much the members may be apparently extended tangentially. As a general rule, the original contact-phenomena remain unaffected near the points of insertion, and the clean-edged long curves and "stepped" shorter curves are readily distinguished. As noted previously, however, and as in the case of hexagonal facetting, such sliding effects always bring a third set of contact-curves into view; so that, when excessive, some confusion may be produced in the primary system (*cf. Sedum acre*, fig. 102). Again, as soon as the amount of "dorsiventrality" and the accompanying sliding-growth becomes considerable, the original spiral "orthostichies" become extremely vague, owing to the difficulty of judging the centres of construction, to which the vascular system does not always afford a sufficient guide; and although theoretically the curvature of this spiral increases with progressive "dorsiventrality," the superposition of the extended members is so close, to the eye, that any deviation from the superposition demanded by the Schimper-Braun hypothesis is inappreciable. It is thus evident that the Schimper-Braun formulae for estimating and describing adult phyllotaxis continue to hold with a considerable amount of accuracy for shoots with markedly dorsiventral members in which the rate of growth is considerably lessened, which constitute, in fact, the normal type of foliage-shoots; but the appearances regarded by Bonnet and Schimper and Braun as primary are now seen to owe their existence to a series of secondary growth-phenomena.

Contact-cycles.—The empirical constructions given in figs. 107 and 109, for systems plotted by Archimedean spirals of the second and third intersection, further suffice to bring into prominence a valuable indication of the relation of the individual members of one cycle of a phyllotaxis system, from the standpoint of their overlapping to form continuous investments of the axis. These relations necessarily hold whatever may be the nature of the spirals used to plot the system; but by using a form of curve which exaggerates the tangential lines of contact, in the manner seen in section of a foliage or flower bud, the relations become

much more striking than in the original log. spiral constructions (fig. 28 (3 + 5)).

Thus the (2 + 3) system constructed by Archimedean spirals of the second intersection agrees sufficiently well with the phenomena
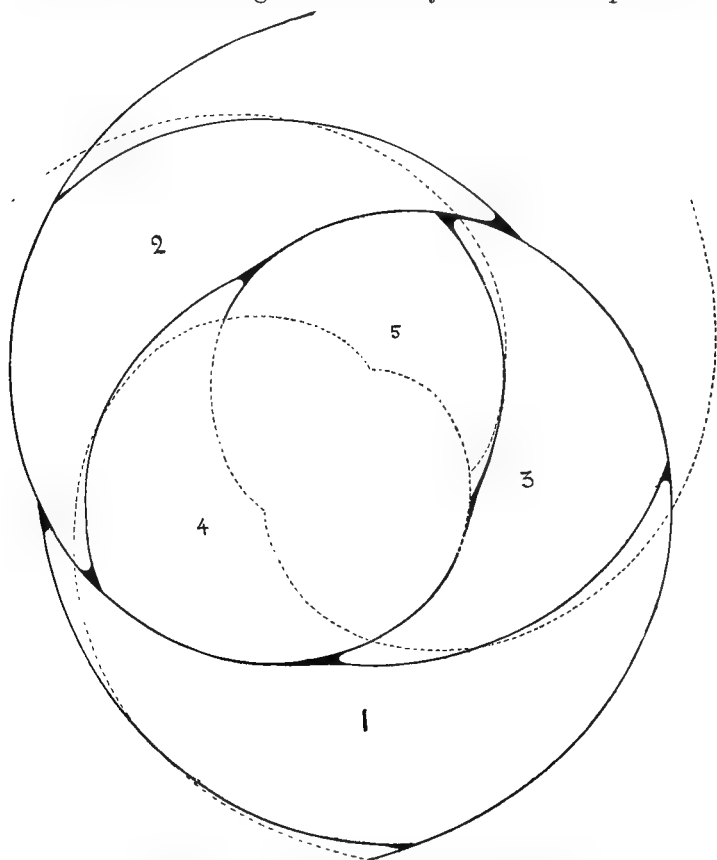

Fig. 107.—Geometrical construction (2 + 3) for contact-cycles, in terms of Archimedean spirals of the second intersection.

observed in the apex of *Sempervivum calcaratum* (2 + 3) (fig. 108), while the seedling of *Nymphaea alba* is also clearly (2 + 3) (fig. 94). Three members form a cycle in contact round the axis, one being half covered, the other two meeting at their pointed angles

x

in the primary construction, but slightly overlapping owing to the secondary sliding-growth effect. The presence of such contact-relations therefore implies a modification of a $(2+3)$ log. spiral system.

Similarly, for the $(3+5)$ system (figs. 28, 109), five members overlap by secondary sliding, although in the original condition two would be half covered and the other three would just touch :
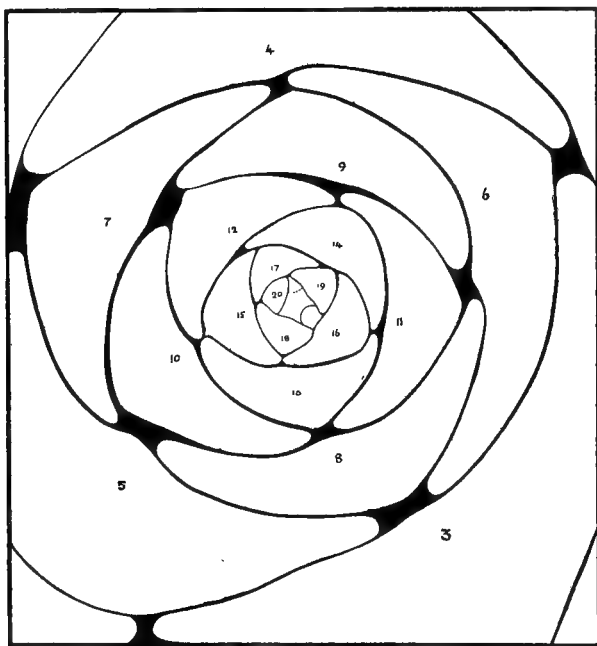
Fig. 108.—*Sempervivum calcaratum,* Hort. Apex of one-year-old shoot, $(2+3)$.

eight members again form an investment everywhere two members deep. In the same manner, by using higher ratios, any spiral constructions will point to the generalisation that the number of the shorter curves is given by the number of members sufficing to form a single investment of the axis, in the case of an unmodified system, or overlapping slightly to form a single closed cycle in the more usual case of flattened members.

It will be at once noticed that such a $(3+5)$ system, for example,

presents a striking picture of the familiar *quincuncial calyx* of the great majority of pentamerous Dicotyledonous flower-types; and given an axis producing such a system of lateral members, the reason for retaining *five* with such constancy to constitute a protective investment becomes increasingly obvious.* These relations are necessary consequences of the utilisation of lines of equal distribution in spiral series, and are of especial interest in connection with the Fibonacci system, in that they give the clue to the number of members requisite to give the best and most equal arrangement, whether in the form of a single cycle or many, so that in dealing with the numerical relations of the parts of asymmetrically constructed flowers it becomes possible to deduce a normal or average type of construction.

The $(3+5)$ system, in an adult condition, and represented by spirals of Archimedes, from the standpoint of the Schimper-Braun formulae, becomes a $\frac{3}{8}$ type, and not a $\frac{2}{5}$ as it is usually reckoned; the error being introduced with the assumption that a specialisation of *five* members implies a cycle of $\frac{2}{5}$, although, as previously noted (p. 15), there was no possible criterion for such an assumption. That is to say, in dealing with a spirally constructed pentamerous flower, the $(3+5)$ system brings the first petal to the front in the gap between sepals 1 and 3, while by regarding

---

* The apparent mimicry of pentamerous flower mechanism observed in the inflorescence of many Composites, in which a calyx-like involucre of five segments is succeeded by a corolla-like series of ray-florets, 5 or 8, and a series of disk-members resembling the spirally arranged sporophylls of a Ranunculaceous type, is thus solely due to the working out of corresponding phyllotaxis rules in the two cases; one full cycle of protective members being succeeded by one full cycle of decorative ones and one or more cycles of reproductive members. If the phyllotaxis system is low, $(2+3)$ or $(3+5)$, the retention of 5 or 8 members in one full cycle of contact is as normal as the retention of full cycles of higher terms of the series in Sunflower capitula. There is no proof that this so-called mimicry is intentional, or even biologically advantageous; it is the necessary outcome of a similar low phyllotaxis system combined with an attempt to reduce the members of each kind to a *minimum*; *cf.* the 5-star flower-like capitula of *Chrysogonum virginianum*, and *Tagetes signata*; as also *Dahlia coccinea*—5 involucral segments, 8 rays, and $(8+13)$ disk-florets—with *Aconitum napellus*—5 sepals, 8 petals, and $(8+13)$ sporophylls.

the quincuncial calyx as a $\frac{2}{5}$ series this proceeding required the assistance of "*prosenthesis.*" Similarly, the fundamental type of a trimerous Monocotyledonous type is a $(2+3)$ system, giving a cycle of three members in lateral contact; so that, when expressed
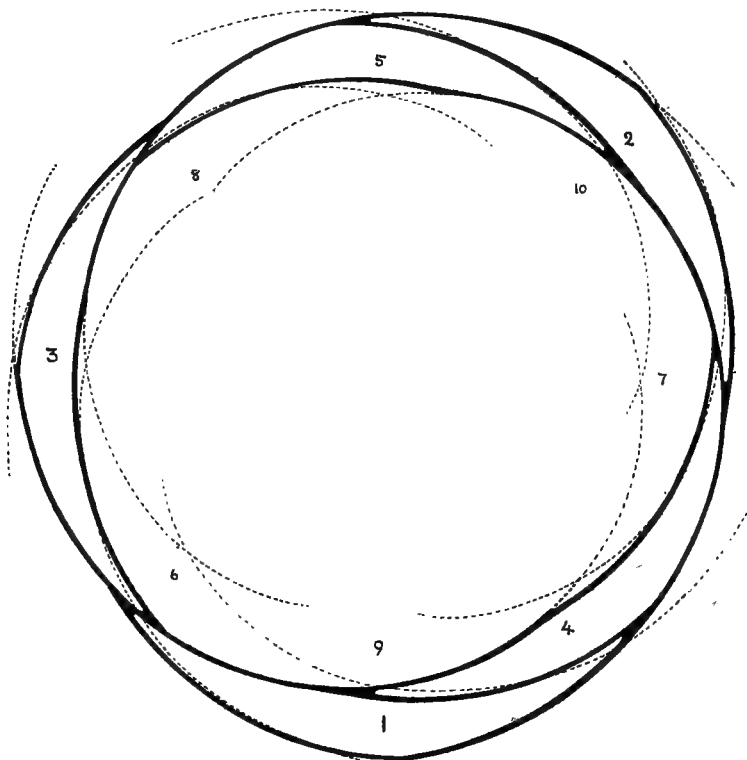
Fig. 109.—Geometrical construction for contact-cycles, $(3+5)$ system, in terms of Archimedean spirals of the third intersection.

in the adult condition by spirals of Archimedes, it would give a $\frac{2}{5}$ divergence formula rather than the $\frac{1}{3}$ of systematists.

The extent, however, to which reliance can be placed on such contact-phenomena in bud-sections remains to be further considered from the standpoint of *varying growth-phenomena* observed in primordia which do not necessarily retain their primary contact-relations.
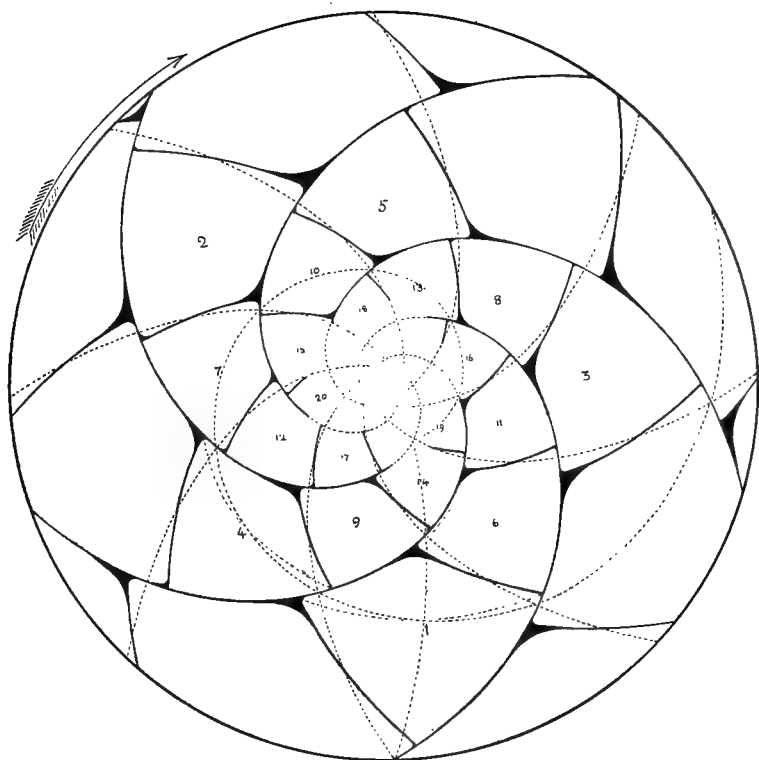
Fig. 110.—Geometrical construction (5 + 8) by log. spirals, with added correction for sliding-growth effect. Cf. *Nymphaea alba*, old perennating stock.

VI. Varying Growth in Lateral Members.

So far, it may be noted, all secondary changes, whether those included under the previous headings of secondary pressure effects or phenomena of bilaterality, have for their result the obliteration of the theoretical log. spiral construction figure, and tend to obscure the primary system. To such an extent, and so rapidly, does this deformation usually take place, that the primary theoretical construction for the distribution of growth becomes increasingly difficult of accurate observation; and it is clear that the special case of bilaterality is but one of a large series of phenomena in which varying rates of growth produce secondary displacement effects. While, in fact, these special cases of "dorsiventrality" and "phyllody" include the disturbances set up in the system consequent on varying rates of growth in different planes in the primordia themselves, other variations are also possible, and may be comprised more especially under two main sections :—

(1) Varying rates of growth between the axis and the primordia.
(2) Varying rates of growth in the primordia at different portions of their length.

That is to say, although the log. spiral construction was founded on a physical and mathematical conception—the assumption of a uniform growth-expansion in the protoplasm of the shoot-apex— it does not necessarily follow that such a uniform rate of growth is actually present to any great extent in the growing-point of any given plant, any more than that all radially constructed stems should prove to be mathematically circular in section. The case of uniform growth, however, requires to be considered first, just

as Newton's first law of motion comes before the second: granted the conditions for uniform growth are known, any variations from these must imply the existence of secondary agencies; and thus, if primordia are once started in a certain direction, and continue to expand at a uniform rate of growth, very nearly uniform also with that of the main axis, the transverse section of the bud at any time would be marked out along orthogonally intersecting log. spirals; and conversely, if the construction observed does not consist of true log. spirals, or the intersections are not orthogonal, it must follow that some secondary change in the rate or direction of growth must have taken place subsequent to the time at which the primordia were laid down, or perhaps became visible. As already noted, a deep-seated faith in this very fact, that a primordium which has been set growing in any given direction will, in the absence of any secondary disturbing force, continue to do so, and so retain its relative station with perfect accuracy, has led to the utilisation of such structures as the Pine-cone, the Aroid spadix, and bractless capitula of Composites as the most typical examples of phyllotaxis.

While a log. spiral construction thus possibly represents the arrangement of certain "lines of force" which are intimately connected with the primary cause of phyllotaxis, the most usual disturbing factor will be the capacity for variation in the *rate* of growth in the members themselves; while alterations in the *direction* of growth will be less marked, but may follow pressure changes as the members become adult, and the action of external conditions of environment, as in the case of the light-induced eccentricity of certain spirally constructed leafy shoots (*Abies*), or still better, a Pine-cone which grows unequally *as a whole* as it bends down after pollination.

It is so far evident that the original phyllotaxis construction along the log. spiral paths conceivably laid down in the protoplasm at the actual growing-point, will be exactly maintained so long, and so long only, as growth remains uniform in the system, and the members retain the same general shape as that of the apex on which they are borne, or tend by mutual pressure to take the form of quasi-squares as seen in section. Such an ideal

construction is not easy to find, owing to the fact that members conventionally recognised as *leaves* always subserve special functions, if developed to any extent, for which they become secondarily adapted ; but the possibility of the conception of such a theoretical and mathematical *primary type* of leaf-member becomes increasingly clear, although now in a sense somewhat different from that of the Ideal Leaf of Goëthe. A remarkably close approximation to such a hypothetical structure is found in the protuberances associated with the primary leaf-points of a typical *Mamillaria*. These conoidal masses, which physiologically replace the primary leaves, are secondary outgrowths which certainly represent a leaf "idea" in the plant, worked out in a primitive mechanical form : their special point of interest is that they convey a very clear conception of the theoretical system, in that they, unlike the primary leaf-appendages, have usually no special tendency to become obviously bilateral. Thus *Mamillaria*, having lost its primary "dorsiventral" assimilating members, in repeating its lateral outgrowth scheme a second time, expresses itself in terms of the simplest possible type of appendage.

Again, if growth in the whole system were uniform in the transverse plane, all primordia, once they were formed, would persist with their bases always in the same plane, and all would appear in transverse section ; but owing to special phenomena of retardation in the main axis, they fall back along it, and the tips of the peripheral members gradually become lost in transverse section of the apex : similar phenomena will also represent the general result of an intercalated "second zone of elongation." It is almost unnecessary to state the case in which growth is uniform between axis and primordium (*dormant centres*), although by assuming the proposition of uniform growth it becomes possible to check the aberration from such a theoretical construction ; and the rate of growth in the lateral members in the transverse direction cannot be much greater than that of the axis at their bases, since their insertions constitute the surface of the axis, though at a higher level the growth may be unequally distributed (*bilaterality*). The longitudinal rate may, however, be considerably greater, and in such case the lateral members close over the apex

and constitute a "*bud*," so that the formation of a terminal
bud-cluster of members and its subsequent expansion thus becomes
a question of the correlated sequence of these growth-variations.
While, then, the general effect of elongation in the main axis
will be to diminish the number of members seen in transverse
section, this may be compensated to a certain extent by extensive
growth in length on the part of the lateral members themselves.
Simultaneously, the approach of adult members to a uniform bulk
results in the secondary production of an effect of spirals of
Archimedes, as already noted.

Hence, the best phyllotaxis patterns will persist in shoots whose
leaves undergo little special modification, and remain either in a
primitive condition as protuberances of rhomboidal section, or are
elongated to needle-like members of similar rhomboidal section.*
Good examples are therefore afforded by *Araucaria excelsa* (fig.
41), *Cryptomeria japonica*, *Pinus Pinea* (primary leaves) (fig.
88), *Cedrus atlanticus* (primary leaves).

Araucaria excelsa (figs. 41, 42).—The leaves retain the rhom-
boidal section of the "square" areas with considerable accuracy,
the orthogonal intersections are fairly well marked, and the
solitary vascular bundles of each member are formed very obvi-
ously at the "centre of construction" (most clearly observed in
fig. 42 $(7+11)$).

Similar phenomena are even better marked in the seedling of
Pinus Pinea (fig. 88); the orthogonal intersections are in some
cases closely approximated toward the centre of the system, and
so clearly is the original construction retained that the disturbing
factors are readily isolated.   These are seen to consist of : (1) the
diminution of tangential growth of members as they reach the
periphery of the plane of section, so that each member of a spiral
path subtends a smaller angle than its successor, except in the

---

* A source of error is also introduced owing to the fact that the primordia,
however perfect in themselves, are inserted on a curved base, and do not,
therefore, extend in a vertical direction.   A longitudinal section is therefore
necessary in order to see which primordia are sufficiently accurately placed
to be taken as typical.   This error tends to be reduced as the apex increases
in diameter ; hence the value of Composite capitula (*Helianthus*) as a type.

case of the first pressure of the primordia to fill their quasi-square areas. Thus, in the specimen figured, the first primordia along a spiral path subtended angles of 47·5°, 52°, 53° (the theoretical angle for a quasi-square of a $(5 + 8)$ system being 51·5°); but nearer the periphery the series fall off to 47°, 40°, 40°, 38°, 35°, respectively. (2) Diminution of radial growth implying progressive "dorsiventrality" is relatively slight, and the sliding effect small, the preceding data suggesting 2° only; and this is due to the fact that the leaves tend to round off at the angles instead of sliding over each other by sharp-edged laminae. (3) Growth of the axis pulls the older members down out of the plane of section; this growth being much more rapid in the seedling of *Pinus Pinea* than in a lateral shoot of *Araucaria*, the compensating effect of a longer needle in the former is not noticed.

Further modification of the primary phyllotaxis pattern ensues with the advance of "dorsiventrality" in the members; in cases in which the leaf-member is markedly dorsiventral, but also elongated, thus constituting a strap-shaped member, the optimum effect will be observed in bud-section (*cf. Podocarpus japonica*, fig. 42). In the more general case, however, the "dorsiventrality" of the leaf-lamina is not regular throughout the whole extent of the member, but it may present the following cases:—

(1) Very great at the base (type of the sheathing leaf-base).

(2) Small in the petiole, or absent.

(3) Considerably exaggerated in the assimilating lamina.

The distinction between lamina and midrib may be small or wanting (*Sempervivum*, fig. 83); or, again, very marked (*Campanula*, fig. 101; *Verbascum*, fig. 36); and in the limit, the former may be complicated by compound segmentation. In such case, the segments of each leaf are restricted to its own rhomboid area, and each leaf is packed or crumpled independently within its own rhomboidal domain (*Ranunculus repens, Nigella, Rheum*). Similar phenomena are observable on a smaller scale in the case of the simple leaves of *Verbascum* and *Campanula* (fig. 101); in the figure of the latter instances of anomalous sliding effects have also been indicated. When the sliding of dorsiventral leaves is excessive, it is clear that new contact-relations will be established in

this part of the bud-section, just as the rounding off of the members from their original contact may also open up another set of contact-parastichies.

Again, since the transverse section must pass through the insertion of the youngest members, the development of the sheathing basal portion as a dorsiventral lamina will often form the most conspicuous feature. *Nymphaea alba* (fig. 94) may be taken as a type: the construction system for the seedling $(2+3)$ is identical with that of *Sempervivum calcaratum* (fig. 108), and in the older members is closely imitated by the theoretical construction (*cf.* fig. 110). The rhombs retain their original position, rounding off somewhat in the petiole, and the dorsiventral lamina sprouts on the younger members and slides among the older ones, cutting off the original lateral contact-relations. Such a figure is, again, practically identical with the bud-section of *Ranunculus repens* (perennating axis), in which the older leaves become compound, but each remains packed within its own area; also with that of *Isoëtes lacustris*, in which the sheathing effect is somewhat greater and the contact much closer; and finally, by complete fusion of the sheathing portion of each leaf around the axis, the construction becomes that of the apex of *Rheum undulatum*.

To see the general effect of the diminution in the rate of tangential growth of lateral members, unmodified by other agencies, a shoot will be required which either bears uniform members in large numbers, or in virtue of a slow rate of elongation in the axis will admit of a large number of members being cut in one transverse section. An example of such a type is found in the rosette of *Sempervivum*; the leaves are uniformly dorsiventral, with no distinction of midrib and lamina, and are retained in an unmodified bud-type of growth. The seedling of *Pinus* should also afford suitable material, as also species of *Sedum*. The general result will be that, if the rate of growth diminishes tangentially, the apparent phyllotaxis system will be raised; while if the tangential rate be increased, the apparent construction system will present a lower ratio system than the one actually laid down at the apex.

Sempervivum tectorum (figs. 2, 3).—The succulent leaves expand

upwards to form a lamina in which "dorsiventrality" is not so excessive as in a more typical foliage-leaf. The growing-point is sunk to the level of the bases of all the leaves, and in spirit-material may be contracted below the insertion of the great majority. Sections of the bud may therefore be compared from different levels (fig. 83, I., II.). A section across the whole bud portion of a full-grown plant shows for the most part five clear curves, pointing therefore to a phyllotaxis system $(5+8)$. The members may be thus readily numbered up along these curves and the system checked to the centre by tracing a hypothetical ontogenetic spiral with a divergence angle of $137°$: the parastichies are, however, seen to be imperfect at the centre, and the overlapping of members in sets of three points to a phyllotaxis of $(2+3)$ (fig. 83, members 28–36). On the other hand, a section which just grazes the top of the axis shows that the actual system in which the members are laid down is $(3+5)$. The apex is broad and flat, the members arise apparently without close contact, and their boundaries are difficult to recognise along the shallow groove which separates them; it is, in fact, only by taking a section that their shape can be defined. There is no doubt, however, as to the construction of the curve-system being $(3+5)$. The explanation of these phenomena appears therefore quite simple; the lamina of the younger members increases rapidly at first, and sliding-growth is sufficient to bring three members into lateral contact; a section taken through the upper part of the younger members in this condition presents the appearance of a $(2+3)$ system. On the other hand, the bulk of the section passes through the outer leaves lower in their course, at a point at which tangential extension is at a minimum; the members thus apparently draw away from each other laterally, and the "8" curves are thus opened up, and the system assumes the form of a $(5+8)$ type with the "5" curves smooth-edged.

A similar effect is seen in species of *Sedum*, in which the members tend to round off and form so-called "centric" leaf-forms. Thus *S. pruinatum* (fig. 103), developing as a $(5+8)$ system, presents the secondary appearance towards the periphery of the section of an $(8+13)$, the "8" curves being now the smooth-

edged ones instead of the "5" series, and the angle subtended by the members diminishes from 37° in No. 66 to 33° in the member numbered 1.

A still clearer example of this effect of the diminution of the angle subtended by older members is afforded by the previously cited seedling of *Pinus Pinea*, on which the angles were carefully measured. The fall ranged from 53°, the maximum angle subtended by young sliding dorsiventral members, to 35° and even 30° at the extreme periphery: from the measurement of theoretical construction diagrams, the angle subtended by a member of a $(5+8)$ system is $51.5°$, that by a member of an $(8+13)$ system 32°. When the small amount of sliding-growth is regarded as in this example compensated by a rounding off of the angles of the leaves, the completeness of the transition is remarkable, and the corresponding apparent alteration in the system is obvious, the "8" long smooth-edged curves being the most prominent feature of the section.*

A similar simple case of great interest is afforded by the comparison of the appearances observed on a closed (wet) and open (dry) cone of *Pinus*. Thus, in *P. austriaca* the scales on the closed cone present facets averaging 12 mm. in diameter, while the cone itself is about 30 mm. in diameter at the widest part; the angle subtended by a scale varies between 45° and 50°, and the apparent phyllotaxis system is therefore $(5+8)$, as seen in the contact-parastichies. When the cone is fully expanded (fig. 5), the diameter of the structure is increased to 60 mm. or

---

* Note that the angles subtended by rhombs of the theoretical log. spiral construction, as also any divergence angles measured from the centre of the system, will continue to hold good for the plane projection of the transverse section, whatever subsequent changes may take place in the rate of radial expansion. While, that is to say, all allowance for the radial retardation of the actual specimen is omitted from the theoretical quasi-square construction, all angular measurements continue to hold for members in the same transverse plane, and thus the calculated divergence angles of the different systems (*Mathematical Note* V.) are the true divergence angles of plant phyllotaxis, however much the radial rate of growth may be affected, since a reduction in the tangential rate, by producing a dome-shaped apex, pulls the members involved down out of the transverse plane.

more, the scale areas remaining the same; the angle subtended by each scale thus falls to 25° or 30°, with the necessary result that the parastichy system now observed is that of (8+13). Similarly, in *Pinus Pinea* the closed cone 75 mm. in diameter presents scale-facets 23–24 mm. across, subtending an angle of 36° to 38°. When correction is made for overlapping, it is clear that the system observed will be (8+13); but when the cone expands to a diameter of 110 mm., the angle subtended by a scale falls to 20° or 25°, which approaches the 19·8° of the (13+21) system.

The apparent contact-curves of the Pine-cone therefore present in themselves no reliable evidence whatever of the actual system with which the carpels were laid down at the apex, beyond the fact that ratios of the Fibonacci series were utilised; the fact that they are the ones really employed is only to be proved by an examination of the curves of the developing shoot-apex; and similarly, it is impossible to say from the mere examination of the free tips of any cluster of leaf-members what the true phyllotaxis system might have been (*cf. Sempervivum spinulosum*, fig. 4, and cones of *Araucaria*). No satisfactory generalisations concerning phyllotaxis can be made for any given asymmetrically constructed plant until the curve-system, or the contact-relations of the members at their insertion on the actual growing-point, has been determined. The system is not necessarily obvious on the adult shoot, and the appearances seen in the case of adult structures need bear no direct relation to the true construction system; the number of parastichies only helps in that it affords a guide to the ratio-series concerned (*cf.* fruiting heads of *Helianthus, Scabiosa,* and *Dipsacus,* in which the assumption of a uniform type of fruit may cause the construction as judged in terms of contact-parastichies to vary one stage in the ratio-series).

The primary curve-system of the growing-point thus tends to be more or less destroyed by the action of the following factors, all of which may be present to a greater or less extent in the production of a typical foliage leaf-bud :—

(1) Diminution in the tangential rate of growth, resulting in the lowering of the angle subtended by the member.

(2) Diminution in the radial direction, giving rise to phenomena of "dorsiventral" bilaterality, including sliding-growth effects.

(3) Secondary elongation of the main axis in passing through the "Second Zone of Growth."

(4) Intercalary growth of petiole formation.

(5) Cessation of growth-activity, leading to the production of members of a constant bulk in the adult condition.

(6) All irregular and local secondary pressure relations in members approaching maturity, producing distortion of spirals in asymmetrical systems, or the true orthostichies in symmetrical constructions (*cf.* fig. 79).

(7) Special differentiation of individual members or portions of them.

So greatly is the discussion of theoretical phyllotaxis limited in its general application to descriptive purposes, that these generalisations may be almost taken as suggesting that the original use of the term *phyllotaxis* as applied to all arrangements and effects, as seen by the eye on young or adult shoots, may after all be retained with great advantage for such phenomena; and the word be still used to express the general relations of members as presented to the eye, and judged either by the loose and approximate method of Schimper and Braun, or preferably by the observation of the more obvious parastichies at any given point; while the true primary system, which is the first visible sign of the hidden forces which initiate new growth-centres in the actual substance of the protoplasm, and which can only be satisfactorily determined by examination of a transverse section at the level of the growing apex, may possibly be preferably restricted to such a term as *mechanotaxis*, in that it indicates in the most concise form the actual *growth-mechanism*, while the parastichies of such a section may further represent paths of equal distribution of growth-energy, existing in a system in which vital energy follows general laws of orthogonal distribution, comparable with those which obtain in the case of manifestations of forms of physical energy, the discussion of which is brought within the range of mathematical conceptions in the mathematical

treatment of mechanics. The otherwise expressive and suggestive term *growth-vortex* may be placed on one side, in that the expression " vortex " has only been used as a geometrical metaphor; though, on the other hand, it is this vortical condition of growth which is the essential character of a shoot-system, and the term would serve to emphasise the standpoint that a leaf is thus to be regarded as a specialised growth-phase of the parent axis, with which, so long as its primary growth is maintained, it remains co-ordinated, as also with its adjacent members, and within certain limitations under the control of the parent growth-centre.

Mathematical Notes on Log. Spiral Systems and their Application to Phyllotaxis Phenomena.

By

E. H. HAYES, M.A.,

Fellow of New College, Oxford;

AND

A. H. CHURCH.

ANY application of mathematical methods to such a subject as that of Phyllotaxis must necessarily be limited by the hypotheses taken as the basis of any conception of the relationship of the phenomena observed, and clearly no further information can be deduced than follows from the original premises.

Thus, as already seen (p. 6), the mathematical conception of a *helix* winding on a cylinder, which was assumed by Bonnet to be a satisfactory interpretation of the facts observed on adult shoots,—although it did not hold for younger ones,—forms the basis of the Schimper-Braun formulae; and the assumption of a spiral with parallel screw-thread led to the adoption of *spirals of Archimedes* when the phenomena were required to be represented as a plane circular system.

Similarly, the introduction of the *Fibonacci* series of ratios by Schimper and Braun naturally brought with it all the mathematical properties of this curious series of numbers, and other observed ratios were readily fitted into similar summation series. But in deducing all the mathematical properties of such combinations, which necessarily follow from the presence of the numbers themselves, it does not follow that the plant, in possibly selecting

such ratios for one reason only, is in any way aiming at all the mathematical consequences of its choice, although they must all necessarily follow; and it thus becomes increasingly difficult to draw the line between the tabulation and interpretation of actual observations and the pursuit of abstract mathematical functions, which rapidly degenerates, as Sachs pointed out, into mere " playing with figures."

So, again, the introduction of *equiangular* spirals as indicating curves of growth necessarily brings with it all the mathematical properties of these curves. One admittedly makes no further advance toward the interpretation of the *causes* of phyllotaxis by the mere introduction of equiangular, ontogenetic, and parastichy spirals.

But if the primary mathematical conception is based on a legitimate foundation, such as that of uniform growth-expansion appears to be, the properties of log. spiral systems become increasingly important as indicating symmetrical or asymmetrical cases of perfect growth, although such spirals may never be measured or even really exist in actual phyllotaxis phenomena, since the modification of the primary construction spirals may be made the subject of subsidiary hypotheses.

While, therefore, the purely mathematical investigation of log. spiral constructions can add nothing to the explanation of the phenomena, it becomes of interest to tabulate the properties of intersecting systems of these curves, in that functions may be deduced mathematically which are not readily apparent in geometrical constructions, just as geometrical constructions, on the other hand, may confirm or make more obvious a mathematical generalisation.

It remains, therefore, to consider what the properties and appearance of such abstract ideal phyllotaxis systems would be, the relation of their parastichies and orthostichies, as also the form of the curves which would represent the homologues of circles inscribed in the orthogonal meshes, and the angles subtended by these in the different systems: the whole set of phenomena thus affording a view of an ideal uniformly expanding system of lateral appendages on a growing axis, which may then

be used as a *Standard of Reference* for the comparison of the phenomena actually observed on any given shoot.

It cannot, perhaps, be too strongly insisted that the log. spiral theory is of value solely in so far that it affords such a standard of reference. The same mathematical conception which assumes the possibility of an abstract uniform protoplasmic growth, also takes cognisance of the fact that protoplasmic growth is never uniform, although the approximation may be very close in certain special cases ; and just how close this approximation may be, the mathematical investigation of the log. spiral systems should help to disclose.

While, again, the mathematical study of these curves may be fairly regarded as outside the province of the botanist, it is clear that the empirical results obtained in previous pages (Part II.) by means of geometrical constructions, more especially in dealing with the convention of *bulk-ratio*, will have little value unless they can be checked by mathematical methods.

NOTE I.—*General Equation to the Ovoid Curve in a Log. Spiral Quasi-Square Mesh—the Quasi-Circle.*

Taking the asymmetrical construction as more primitive and mathematically a more general case of construction, of which whorled symmetry is only a special case, the system can be discussed mathematically in the following terms :—

In an $m:n$ network of logarithmic spirals, the equation of one set of spirals may be written,

$$n \log r = n \log c + m\theta + (2k-1)\pi,$$

and of the other,

$$m \log r = m \log c - n\theta + (2l-1)\pi ;$$

where k, l, are any integers, positive or negative.

Values of k differing by m refer to consecutive turns of the same spiral, and similarly values of l differing by n.

The " centres of construction " of the network are given by the intermediate spirals,

$$n \log r = n \log c + m\theta + 2k'\pi,$$

and $$m \log r = m \log c - n\theta + 2l'\pi.$$

To find the curve inscribed in a mesh of the network analogous to a circle inscribed in a square, use the orthogonal transformation $\log r = x$, $\theta = y$: also put $\log c = a$.

The equations of the two sets become,

$$nx - my = na + (2k-1)\pi,$$
$$mx + ny = ma + (2l-1)\pi,$$

so that in the transformed system the meshes are equal squares of side $\dfrac{2\pi}{\sqrt{m^2+n^2}}$.

Consider the mesh whose sides are given by $k=0$, $k=1$;
$$l=0,\ l=1.$$

Its "centre of construction" is at the intersection of the spirals given by $k'=0$, $l'=0$, i.e. is at the point $r=c$, $\theta=0$.

The sides of the corresponding square in the transformed system are,

$$nx - my = na \pm \pi,$$
$$mx + ny = ma \pm \pi,$$

and its centre is at the point $x=a$, $y=0$.

The equation of the circle touching the sides is

$$(x-a)^2 + y^2 = \frac{\pi^2}{m^2+n^2}.$$

Transforming back, the equation of the required curve is found to be:—

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

The logarithm is the natural logarithm, and θ is measured in circular measure: when the logarithm is the tabular log and θ is measured in degrees the equation may be written:—

$$\log r = \log c \pm 1.36438 \sqrt{\frac{1}{m^2+n^2} - .000030864\theta^2}. \quad \text{(II.)}$$

The point corresponding to the centre of the circle is $r=c$, $\theta=0$, i.e. is the "centre of construction."

Since all the meshes are similar, differing only in size, the above equation will apply to any mesh, if c is the distance of the centre

of construction from the origin, and θ is measured from the line joining these points. The curve touches the sides of the mesh where they are met by the two intermediate spirals which determine the " centre of construction."

From the character of the above equation it follows that *the curve is symmetrical with respect to the line joining the origin to the centre of construction.*

This mathematical deduction is of the greatest botanical interest, in that it brings out the remarkable fact that every lateral primordium is primarily *bilaterally symmetrical* with regard to a *radius* drawn through the centre of construction and the centre of the main axis ; and thus, *whether in a whorled or spiral phyllotaxis system, its primary structural peculiarities will be identical.* Thus, no change whatever is involved in the properties or shape of the lateral members themselves, when the phyllotaxis system passes from an asymmetrical construction to a symmetrical one ; that is to say, change of symmetry in the radial axis system does not directly affect the symmetry of the appendage, and whatever the curve-ratio of the construction, the leaf-members would be equally *isophyllous*, although eccentric growth of the whole shoot, by affecting the shape of the ovoid curve itself, involves *anisophylly*. On the other hand, the contact-pressures of adjacent growing primordia, which cause them to approach the shape of the quasi-square meshes, result in making the primordia *secondarily* asymmetrical to a certain extent when the curve-system is asymmetrical.

The general result of this mathematical investigation is to establish the fact that certain essential properties are common to all leaf-primordia expressed as quasi-circles ; and these may now be expressed in botanical phraseology.

I. All such appendages are *bilaterally* symmetrical about a median line, the radius drawn through their own centre of construction and the growth-centre of the axis itself. The appearance of radial flattening to which they are subject in the main growing system thus exaggerates this symmetry in two orthogonal directions—one a radius of the system, the other a circular path of the same central system.

II. The appendages further possess that peculiar attribute called by Sachs their *dorsiventrality*—a term which, as previously shown, requires to be taken in a purely metaphorical sense, and which only holds its own in that it is as useful as any other expression for indicating the fact that the members possess two unlike surfaces, and that these are *upper* and *lower* surfaces, a point not implied by the term *bifacial*. The form of the quasi-circle shows that the peripheral portion of the appendage, as seen in section, is larger than the interior part; so that, in carrying these members over the slope of a dome-shaped apex, the exaggerated side becomes the lower surface of the leaf: this again being the mathematical consequence of the fact that the growth-centre is transferred to a point nearer the inner side of the curve.

III. The term *isophylly* indicates still more concisely that property of the members in which the bilaterality of the appendage is expressed in the form of two equal sides about an axis of the member in the tangential plane of the system, and is usually applied to the shape of the lamina surface rather than to its section: this again is equally a mathematical property of a growing primordium possessing such a curve-section.

The mathematical investigation thus shows that all primordia, whatever value be given to m *and* n, *present these properties as fundamental and unavoidable features of construction. Every appendage is mathematically bilateral, dorsiventral, and isophyllous, with regard to the shape of the curve and the position of its centre of construction.* These are mathematical necessities of the type of growth-system adopted by the shoot as a centric growth-centre producing a rhythmic series of subsidiary centric growth-centres. A growing system might evidently have one such centre or more than one. One is the simplest case, and as a matter of observation is the general rule; on the other hand, the case of multiple growth-centres is included under the botanical title of *fasciation phenomena.* Here at last is a definite foundation on which to build the morphology of the shoot; and it now becomes possible to draw a distinction between the necessary *properties* and the *accidentia*, or phenomena of subsequent adaptation. Why the

shoots of higher plants should have evolved such a growth-construction as a means of increasing the body surface remains unsolved; but so long as a shoot possesses a persistent embryonic growing apex, some such construction would appear necessary : in fact, if the growth-centre is to remain a point, *dichotomy* would be the only simple alternative. Why, again, certain curves should be selected, their *number, ratio, inequality* or approximate or actual *equality*, still constitute further problems apparently hopeless of any immediate solution, although teleological suggestions may be put forward to explain the frequency of simpler forms of symmetry, *e.g.* $(2+2)$ and $(1+1)$. But granted the initiation of such construction systems by the plant itself as the elaborated response to some general co-operation of external agencies, these fundamental characters are *mathematical consequences*, however much or little the subsidiary action of special influences may tend to subsequently mould the growth-forms thus initiated by the shoot-apex. The influence of external environment, of which so much is expected in these days by enthusiastic materialists, must have something to act upon : the use of the favourite expression *adaptation* implies the pre-existence of a certain *something* which can be modified ; and just what this something is, and how far it goes, is thus defined in mathematical terms by such a generalisation as that of the growing system of growth-centres.

Leaf - appendages in centric growth - systems are therefore *bilateral, dorsiventral, and isophyllous,* not from direct relation to the action of any such agencies as gravity or vertical light, but from the mechanical laws controlling the distribution of the material substance of which they are composed. Further, a plant shoot builds such primary appendages of one kind only ; whether they are all to be classed under the general term *leaf-members,* or whether this term is to be restricted to the specialised assimilating organs, is a matter of little consequence. The abstract *Urblatt* of Goëthe is now exchanged for an actual concrete and mathematically defined appendage, *the quasi-circle primordium,* and the futility of any discussion as to the priority of foliage-leaf or sporophyll becomes obvious.

NOTE II.—*Mathematical Orthostichies in Log. Spiral Systems.*

To obtain a collinear intersection of m and n spirals, *i.e.* a second point of intersection in the same straight line with the origin, it is clear that in the Fibonacci series, for example, it is only when $m : n :: \sqrt{5-1} : 2$ that such an intersection will take place at infinity.

But with m and n *finite integers*, radially superposed intersections will take place; and taking the case of m spirals crossing n, the nearest point collinear with the origin and any given point on the same side of it will be the (m^2+n^2)th term: that is to say, in the general case in which m and n have no common factor.

Thus, in the system $(3+5)$ a true orthostichy will exist between any member taken as 0 and the $(9+25)=34$th. In the case of *Sempervivum tectorum*, for example (figs. 1, 2, 83), the contact-parastichies at the apex being $(3+5)$ (fig. 83), the line drawn through No. 1 and No. 35 (fig. 2) should be mathematically a radius, and a true orthostichy line to produce which the onto-genetic spiral would wind 13 times $\left(i.e.\ \dfrac{13}{34}\right)$.

It will be noticed that such points are beyond the range of the construction diagrams, which only include a portion of one revolution of the pair of generating log. spirals; and also beyond observation on the plant, owing to the fact that minute differences in the growth of older leaves would suffice to produce slight displacements which would destroy the effect of these mathematically straight lines. For practical purposes these true orthostichies pass beyond the limit of consideration, but the fact that such are possible is still of botanical interest; while the curious relation of such an empirical formula of the Schimper-Braun series to the actual construction in the case of *Sempervivum* is noteworthy. The phyllotaxis may here be thus accurately written in the Schimper-Braun terms $\dfrac{13}{34}$, but such a formula can only be deduced from the consideration of the properties of a $(3+5)$ system, and not from any inspection of the external characters of the leaf-arrangement on the plant itself, in which superposition effects

are increased by the gradual transition to apparent spirals of Archimedes as the members attain a uniform bulk ; nor could any approximation to the eye of a $\frac{13}{34}$ orthostichy line be ever taken as an indication of a $(3+5)$ apical construction.

Similarly, other orthostichies may be tabulated :—

$$
\begin{aligned}
(m^2+n^2) \text{ for } (\ 1+\ 2) \text{ system} &= \quad 5 \\
(\ 2+\ 3) \quad ,, \quad &= \quad 13 \\
(\ 3+\ 5) \quad ,, \quad &= \quad 34 \\
(\ 5+\ 8) \quad ,, \quad &= \quad 89 \\
(\ 8+13) \quad ,, \quad &= \ 233 \\
(34+55) \quad ,, \quad &= 4181 \text{ etc.}
\end{aligned}
$$

The first case $(1+2)$ is of interest, in that it should be the phyllotaxis of *Pandanus* and *Cyperus*, which it obviously is not (*cf.* figs. 51, 59*b*). This has been suggested as due, as in the case of *Sempervivum*, to the change in the spirals consequent on the rapid attainment of approximately equal radial depth (fig. 51). The last case being that of the capitulum of *Helianthus* taken as a type (fig. 15), in which the system was only carried for between 6–700 members before it broke down ; so that even if this type of formula were retained in the descriptive account of phyllotaxis, it becomes quite useless in all high series.

Note III.—*The Form of the " Ovoid" Curve.*

From the equation of Note I., the curve for any given system may be plotted out. Five such curves, those for the

> asymmetrical $(3+5)$,
> asymmetrical $(2+3)$,
> symmetrical $(2+2)$,
> asymmetrical $(1+2)$,
> symmetrical $(1+1)$,

are represented in fig. 111.

It will be noticed that the form of the $(3+5)$ quasi-circle scarcely differs to the eye from a circle, and this approximation is shown by the dotted line. The curve is, however, slightly

flattened in the plane passing through the origin, and is thus broader than long; that is to say, the primordium of such a system is already by construction slightly "dorsiventrally"
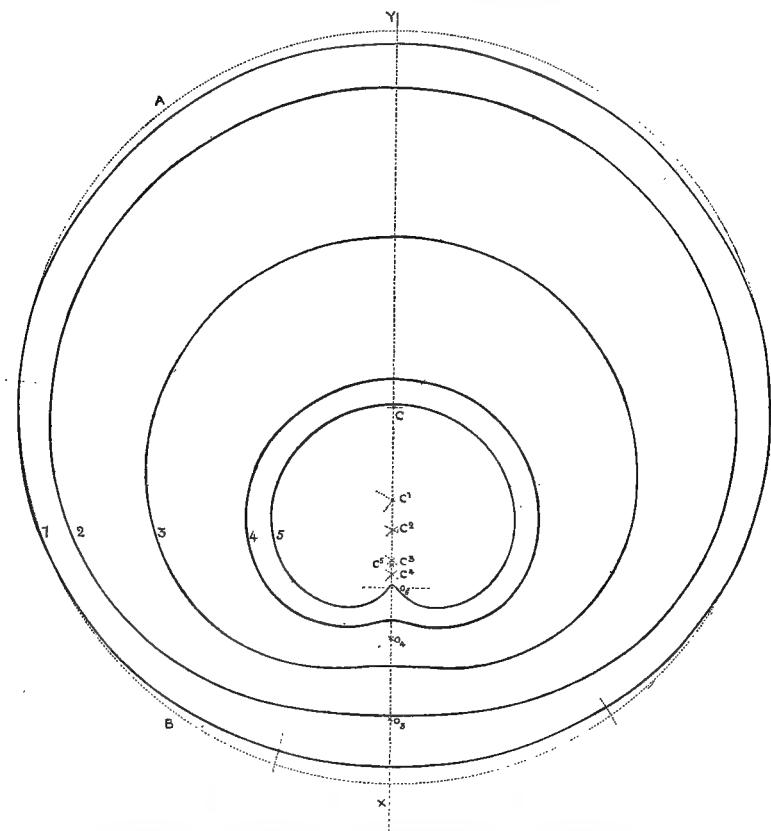

Fig. 111.—Set of five quasi-circles of the systems (3+5), (2+3), (2+2), (1+2), (1+1), arranged for convenience of illustration in diminishing series, 1, 2, 3, 4, 5 respectively, along the plane of median bilaterality XY.

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

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

bilateral in the median plane. Thus the extreme breadth of the curve as plotted was 11·796 inches, the extreme length 11·304

inches ; the curve thus approaches a circle in which the amount of error is not greater than $\frac{1}{19}$th of the radius.

In all higher systems the approximation to the circle will be successively closer, so that, as previously pointed out, the use of circles in the quasi-squares of any system above $(3+5)$ is beyond any error of constructing a small diagram. The relation of the curve to its " centre of construction " homologous with the centre of the circle has also been previously indicated, since it is readily noted on the geometrical diagram by taking the point of intersection of the intermediate spirals.

The $(2+3)$ curve, again, shows a marked distortion, and the flattening on the side towards the origin is excessive, the general outline obviously differing from a circle. This is still further exaggerated in the $(2+2)$ curve, in which a distinct dimple begins to appear at this point (fig. 111, III.), and the " centre of construction " shows still greater displacement. The $(1+2)$ curve becomes distinctly kidney-shaped, with the centre of construction very close to the depression (fig. 111, IV., $C^{iv.}$); and the limiting case is met with in the $(1+1)$ curve (fig. 112, A, the centre of construction being at C').

It thus follows that lateral primordia may be represented in theoretical construction diagrams as circles, within any error of drawing, in any system from $(3+5)$ upwards. In lower systems the bilaterality of the ovoid is very marked, so much so, in fact, that the occurrence of such a form at the apex of a plant-shoot would not readily strike the observer as in any sense due to the production of a primordium, the section of which would be homologous with a circle, and within its sphere of growth possessed of the same physical properties.*

· * The same curves, or similar figures for any given ratio system whatever, may be easily drawn within the error of drawing by a simple geometrical method. For example, to draw the curve for the ratio 3 : 4, make a curve-tracing for this ratio from the circular network of squares (p. 53), and with the curve-tracing mark out a quasi-square mesh of the system. Divide this into 12 equal parts in either direction by describing 11 intermediate spirals in each direction, and into these smaller squares transfer square by square the circle inscribed in a true square similarly divided into 144 meshes, the points where the circle cuts the meshes being judged by the eye with sufficient accuracy.

Since the curves of the higher ratios so nearly approach a circle, the lower ones figured are really the only ones which possess a special interest.

NOTE IV.—*Bulk-Ratio.*

The bulk-ratio, defined as the ratio between the sectional diameter of the lateral primordium and that of the axis at the point at which the member was *apparently* inserted, was taken as represented with approximate accuracy by the ratio of the radius of a circle empirically described in a quasi-square mesh to that of the circle drawn through the centre of the former one (p. 88), and from such empirical constructions the angle subtended by a primordium of any given system was approximately measured, well within any degree of observation error on the plant.

Since there can evidently be no ready comparison of bulk-ratio between the circular section of an axis and the ovoid section of a lateral member, this method will prove sufficiently accurate. But it is possible to approach the subject from a different standpoint. Thus, the angle subtended at the origin by each ovoid primordium may be calculated mathematically, and this angle may be compared with the empirical geometrical construction.

Systems of m and n spirals.	Data for true curve.		Data for empirical circle.		
	Angle subtended $= \dfrac{360°}{\sqrt{m^2+n^2}}$.	Sine of half angle.	Bulk-ratio approximated from geometrical construction.	Corresponding sine of half angle.	Corresponding angle; *cf.* p. 89.
$(1+2)$	161°	...	...	...	...
$(2+3)$	99° 52′	...	...	...	...
$(3+5)$	61° 44′	·513	1 : 2	·500	60°
$(5+8)$	38° 10′	·327	1 : 3	·333	38° 57′
$(8+13)$	23° 35′	·204	1 : 5	·200	23° 5′
$(13+21)$	14° 35′	·1269	1 : 8	·125	14° 20′
$(21+34)$	9°	·0785	1 : 13	·0769	8° 48′
$(34+55)$	5° 34′	·0486	1 : 21	·0476	5° 26′
$(55+89)$	3° 26′	·0300	1 : 34	·0294	3° 24′
$(89+144)$	2° 7′	·01855	1 : 55	·01818	2° 5′
$(144+233)$	1° 19′	·01147	1 : 89	·01124	1° 17′

The angle subtended by a primordium belonging to any system of orthogonally intersecting log. spirals is given by the following formula :—

$$\frac{2\pi}{\sqrt{m^2+n^2}} \text{ or } \frac{360°}{\sqrt{m^2+n^2}}.$$

The bulk-ratio for circular primordia was represented by the *sine of half the angle subtended at the origin* ; the same expression may be regarded as representing the approximate bulk-ratio in the case of the ovoid curves which so nearly approach circles.

From the above table it will be seen that the difference between the angles subtended by the ovoid curves and those subtended by circles having the respectively simple bulk-ratios obtained approximately by geometrical construction is a very small one.   Such an error is quite within any limit of construction error in small diagrams, and is far within the error of checking systems in the case of the plant, in which, as previously noted, the construction adjustments that must be made in the bulk-ratio before a new spiral path is introduced must be necessarily often very considerable ; so that for practical purposes the integral bulk-ratios of the respective systems may be taken as sufficiently accurate statements of the phenomena observed.   The empirical geometrical method of estimating the bulk-ratio of any given system is therefore sufficiently reliable, if the convention can be of any assistance, and does not involve any special mathematical knowledge.

NOTE V.—*The Oscillation Angle.*

Taking the construction of a constant asymmetrical spiral phyllotaxis system as the result of adding members at a constant *divergence* angle, or as a phenomenon of growth oscillation,—a convention which only holds, however, as has been previously made clear, for integral ratios only divisible by unity as a common factor,—the measurement of the true angular divergence of the members of the systems constituting the Fibonacci series becomes of special interest from the standpoint of comparison with the helical divergences of the Schimper-Braun-Bravais convention.

The angle is given by the formula:—

$$\frac{2mn - m^2}{m^2 + n^2} \text{ of } 360°.$$

Thus for $(1+ 2)$ the divergence angle $= \frac{3}{5}$ of $360° = 216°$ or $144°$

$(2+ 3)$	,,	,,	$\frac{8}{13}$	,,	$= 138°\ 27'\ 42''$
$(3+ 5)$	,,	,,	$\frac{21}{34}$	,,	$= 137°\ 38'\ 50''$
$(5+ 8)$	,,	,,	$\frac{55}{89}$	,,	$= 137°\ 31'\ 41''$
$(8+13)$	,,	,,	$\frac{144}{233}$	,,	$= 137°\ 30'\ 38''$

while the limiting angle

$$\frac{\sqrt{5}-1}{2} \qquad\qquad\qquad = 137°\ 30'\ 28''$$

The "ideal angle" of the Fibonacci series remains the same as in the Schimper-Braun series; but the angles for lower members of the series are not only very different from the conventional series, but they are definitely very much more like the angles obtained in measurements of plant specimens.

The standpoint of the Bravais, that there might be quite reasonably only one angular divergence for normal Fibonacci phyllotaxis, and that one the "ideal angle" of Schimper, is thus seen to be well within the experimental facts. Since, it may be again pointed out, these angles hold for *growing* systems, they do not hold for systems which show progressive cessation of growth; but so long as growth proceeds uniformly in the system, that is to say, the nearer the apex of a plant approximates uniform growth, so will these angles be the true angles of phyllotaxis, and will be found well within any error of observation on the plant. The $(1+2)$ system alone differs from the ideal angle by about $7°$, and as already noted, a $(1+2)$ system which can be regarded as approximately exhibiting uniform growth is not readily obtained, owing to the effect of growth-retardation and secondary cessation. It will be noticed that already at the $(2+3)$ system the "ideal angle" may be attained within an error of about one degree (*cf.* fig. 94) in a primordium which subtends $100°$; while an error of one per cent. is practically beyond consideration in dealing with the plant. A slightly higher ratio $(5+8)$ gives the "ideal angle" within a theoretical error of *one minute*. While the possible

physical accuracy of construction which is represented by an (8 + 13) system, probably the highest ratio ever *directly* initiated at the apex of a shoot, suggests that in the extremely minute growth-centre in the first zone of growth, beyond any visible primordia, the mechanism at the hypothetic growth-centre might become a question of even molecular aggregation, and thus may be again fairly comparable to phenomena of crystallisation.

For practical purposes the angle $137\frac{1}{2}°$ may thus be assumed approximately constant for all Fibonacci systems beyond $(2 + 3)$. For this system the value $138 \cdot 5°$ obtained from the geometrical construction is sufficiently accurate to suggest that similar constructions will be equally satisfactory in the case of anomalous ratios. For example, the system $(7 + 11)$ of *Araucaria excelsa* as represented on a geometrical diagram gave $99 \cdot 6°$ for the oscillation angle, while the calculated divergence was $99 \cdot 53°$.

So long, therefore, as a log. spiral construction is postulated, the botanist may investigate the subject without any need of special mathematical knowledge; the simple geometric diagrams taken in the preceding pages being far within any error of observation on the plant, and having the additional advantage of presenting a difficult subject in a simple and concrete form.

NOTE VI.—*The Fibonacci Series.*

The most remarkable feature in connection with plant phyllotaxis, whatever view be taken of its origin or final cause, is after all the predominance of the numbers of the Fibonacci series. That the series is not by any means indispensable is shown by the wide range of variation into anomalous systems, and the complete elimination of the series in the case of symmetrical constructions. The following two points may be here brought forward to throw light, if possible, on this peculiarity of plant construction :—

I. The numbers of the construction curves must be *integers* and *low numbers*, or else the lateral appendages will be relatively very small; and as a matter of fact in all seedlings the lateral appendages are relatively large as compared with the main axis. These are facts derived from observation of the plant, and from the conception of bulk-ratio,

Next, as a matter of observation also, the ratio of the construction curves must not show any great inequality; on the contrary, a very general approximation of equality in the numbers of the curves appears to be the general rule. The rule appears to be that one number must not be more than double the other : this being again the generalisation of Schimper and Braun, which places the ratio 1 : 2 as the limit. The highest range of this type of ratio has been recorded as (3 : 6) for a trijugate plant of *Dipsacus.** Hence the choice of higher plants is really restricted in the great majority of cases to such combinations as—

> 1 : 1
> 2 : 1, 2 : 2, 2 : 3, 2 : 4
> 3 : 3, 3 : 4, 3 : 5, 3 : 6, etc.,

these being the only low combinations possible. Taking these nine ratios, it will be observed that *three* are cases of *true symmetry*, *three* are Fibonacci pairs, while the (1 : 1) may also be regarded as in the Fibonacci series; the (3 : 4) is the commonest anomalous ratio, and the (2 : 4) the common " bijugate " one. Taking only these simple expressions, then, the balance of construction is in favour of the Fibonacci series, which when once laid down lead on naturally to higher expansion derivatives of the system, which follow with mathematical precision as consequences of the properties of systems of intersecting spiral curves. A predominance of Fibonacci ratios, so far as asymmetrical phyllotaxis is alone concerned, would thus be expected to obtain; and this quite apart from any possible biological utility of the series or of a spiral distribution or building mechanism, prejudices in favour

---

* There is a suggestion that other ratios occurred in lower types : a wider range of ratio, *e.g.* 1 : 3, occurs in Mosses, as also in the apical cell of the Fern ; ratios of 1 : 4 also in Florideae. These and a few isolated cases (*cf. Cheirostrobus,* Scott) require to be taken separately : the general standpoint obviously being that all mathematical possibilities should be equally expected to occur, and the fact that certain types obtain in present vegetation rather than others may indicate the gradual effect of natural selection on the construction mechanism, the general trend appearing to be, as already indicated, towards either symmetry or ratios of the Fibonacci series.

of which standpoints have been so frequently built up by a use of the *post hoc ergo propter hoc* line of argument.

II. It will be seen to follow from the remarkable property of the Fibonacci ratios—that the ratios of any successive pair are almost constant, and that $3:5:8:13:21$, etc., with a considerable degree of accuracy, so far as integers are alone concerned, as again is the case in the curve-systems of phyllotaxis—that in the case of all expansion systems derived from an initial pair with a view to lessen the relative size of the lateral appendage, these numbers alone give a *minimum loss of regularity* at every step in the change; while with any other series, such as $3:4:7:11$, etc., the transition would involve a large step and a small step alternately. In other words, any aim on the part of the plant at uniformity of construction in a system which is liable to change by the addition or loss of paths, as in cases of very active growth (*cf. Helianthus*) in which new curves are continually being added to reduce the relative size of the lateral member as the growing-point gains in bulk, can only be satisfied in one of two ways. Either the plant acquires true symmetry and maintains it by adding curves in either direction simultaneously (*cf. Equisetum*), or that asymmetrical system must be adopted in which the expansion transitions can be effected with the *least loss of regular construction*. The system which fulfils these demands is the Fibonacci series; and from merely numerical reasons there appears to be a balance in favour of the chance of the initiation of curves in these ratios to begin with. So that, granted the asymmetrical condition of phyllotaxis is the primitive one, the general occurrence of curve-ratios in the Fibonacci series would be mathematically expected to occur. The choice of the plant for optimum phyllotaxis relations, in fact, lies between *true symmetry* and the *Fibonacci type of asymmetry*; hence when true symmetry obtains the special numbers of the latter sequence are no longer to be noticed as more usual than others, and all other systems become rightly classed as *anomalous*, in that they deviate from the two optimum conditions. One thus becomes mathematically justified in regarding anomalous variations, including the peculiar bijugate constructions, as expressive of a state of degeneration in the mechanism of shoot

construction; and when this condition becomes the rule, it is possibly the result of unfavourable conditions of environment, and may thus be correlated, as in the case of Cacti, etc., with other xerophytic peculiarities.

NOTE VII.—*Continued Fractions.*

Since the time of Schimper and Braun much importance has been attached to the formulation and presentation of the ratios commonly found in plants in the form of a summation-series presenting certain mathematical properties; the ratios being successive values of the stages of a continued fraction, the limiting value of which became expressed as an "ideal angle." Hence mathematical statements became read into the subject with which Botany has nothing whatever to do. The formation of these summation-series from observation of the plant kingdom, which represents the great botanical discovery of Schimper on which all his contributions to the theory of phyllotaxis were based, is a *mathematical consequence of the phenomena of intersecting spiral curves* radiating round a central point. The preceding geometrical diagrams have rendered this sufficiently obvious (*cf.* figs. 25, 26). Thus, if a certain number of curves cross another set, the same points of intersection will be mapped out by two other sets representing the sum and difference of the first set (*cf.* p. 56); or, if m curves cross n, $(m+n)$ and $(m-n)$ curves will also pass through the same points and form diagonals of the original meshes : four terms of a summation-series are thus involved, and other terms may be obtained in the manner already described. Given the intersecting curves, the mathematical manipulation and description of continued fractions becomes a feature with which Botany has nothing to do, nor is it at all helpful in any direction. Such expressions may attract the mathematician, but they repel the botanist, and it is hoped that the method of constructing geometrical diagrams of the types indicated, on which the relations of the numbers can be more directly traced, will tend to eliminate these expressions from botanical literature, together with the curious prosenthesis formulae of older writers and the Dachstuhl angles of a later school.

NOTE VIII.—*Sliding-Growth.*

From Note I. it is clear that each primordium is primarily bilaterally symmetrical about two axes, represented respectively by a radius of the system and a circle passing through its centre of construction; and so long as the primordia are free from adjacent members each will retain this form, except in so far as it becomes affected by secondary alterations in the rate of growth in these respective directions; and this holds for the case of symmetry and also for the more general case of asymmetrical construction; that is to say, in an asymmetrical construction in which no contacts are made, no sliding-growth effect takes place, and the leaf-members would be horizontally extended and isophyllous on the adult cylindrical shoot. But as soon as the members make lateral contact, the mathematical conditions undergo a change, as previously noticed, the members become represented by oblique rhombs, obliquely placed and anisophyllous; the packed leaf of an asymmetrical system thus becomes *secondarily* an asymmetrical structure, while in a symmetrical system, on the other hand, it still retains its original symmetry in relation to the radial and circular paths of the system : in other words, the free portion of a leaf in a spiral system is free to obey its structural properties as a quasi-circle, but so long as it is packed and makes close contact with adjacent members its growth-form becomes *distorted* into the form of a quasi-square rhomb. In a spirally constructed bud, therefore, with leaves growing more or less in contact below, but free from one another above, as the expression of a conoid growth-form which was initiated from a point and extended until it reached the product of an adjacent centre, the change from the lower distorted region to the upper symmetrical part, when this takes place throughout the whole system, will convey the impression that a slight twist has taken place in the members, as the tangential diagonal of the oblique rhomb changes to a true circular path. It is this appearance of a tendency to a readjustment on the part of the free portion of the appendage which gives the primary tendency to *slip* in the bud, and the phenomenon provisionally included under the term

z *

"sliding-growth" is essentially nothing more than the appearance of these circular paths in the spiral asymmetrical diagram. That this appearance of sliding-growth effect tends to change the "spiral of dorsiventrality" into a circular path has already been shown, but this is not a "biological adaptation"; it is not the direct result of any external conditions of environment; it is simply the expression in the free primordium of those fundamental properties of a quasi-circle which become masked so long as the primordium tends under pressure to take the properties of a quasi-square.

The *primary* sliding effect is thus defined as the result of the free portion of all appendages produced in contact-systems attempting as they become free to return to their original position of symmetry along radial and circular paths. The occurrence of oblique spiral symmetry in a contact-system is a phenomenon of distortion, and all such effects are increased by any secondary growth-relations of the appendage, either as it becomes larger above its insertion, or as it tends to tangential extension, as in the differentiation of the leaf-lamina from the midrib.

It is of interest, therefore, to compare these deductions from the mathematical equation with the facts observed in the plant when plotted into a large drawing under the camera lucida; it must, however, be remembered that in the section at the level of the growing-point transitional stages will be found, but if the members make contact from the first, the amount of "sliding-growth" is fairly constant (*cf.* figs. 101, 106), and may be put into the theoretical diagram with a log. spiral, as in fig. 100; the amount of sliding-growth which may be regarded as *normal* for a given asymmetrical construction being the amount which will make the tangential diagonal of any appendage a circular path.
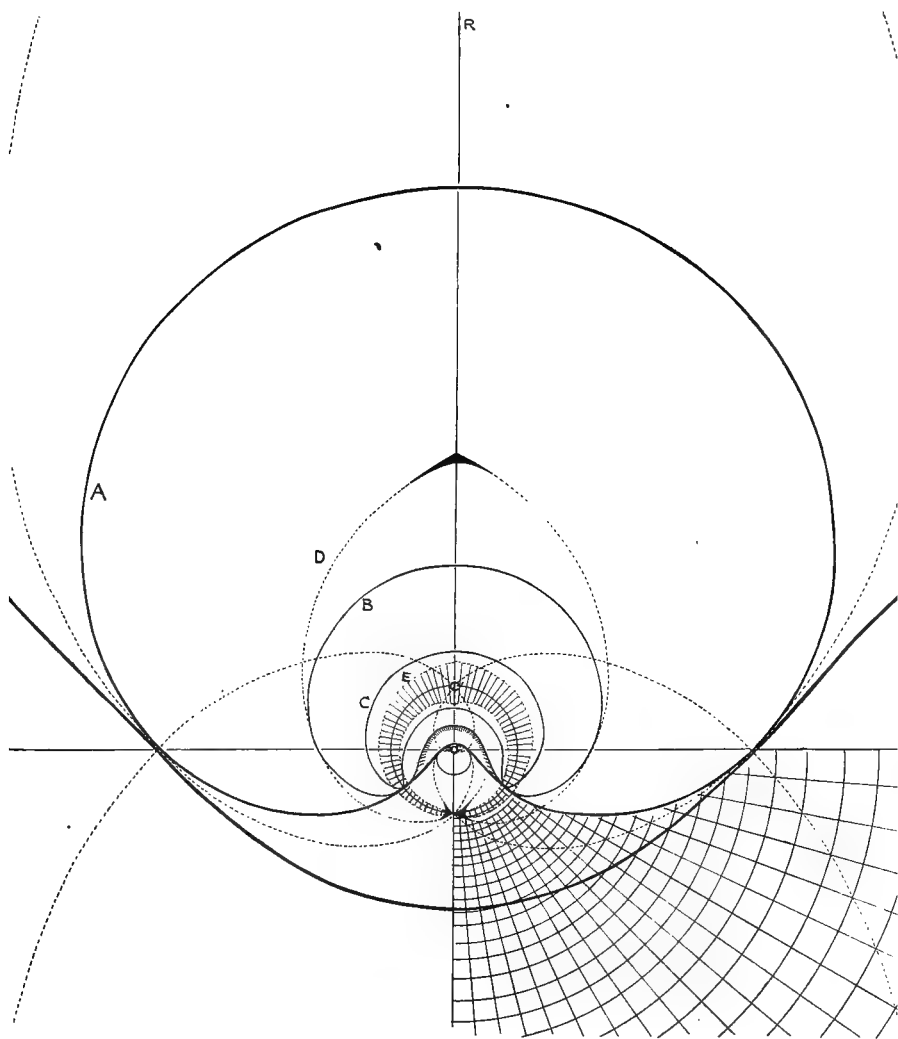
Fig. 112.—Distichous (1+1) phyllotaxis system. Geometrical construction for uniform growth, with derivative curves showing radial retardation ; A, B, C, free members ; D, E, " packed " members.

General Conclusions.

I. THE log. spiral theory, as already indicated,* is put forward solely as a mathematical conception, admittedly gratuitously introduced into plant-morphology, as a fundamental hypothesis founded on a mathematical theory of centric growth (Part I., p. 16), and is intended to replace the helical theory of Bonnet, ⸳ ⸳ ⸳ ⸳ ⸳⸳ which, being deduced from an ideal adult construction, was only required to imitate appearances of leaf-distribution on a full-grown shoot. In the preceding pages this new view of the growth of a plant-shoot and its appendages from one "growth-centre" has been elaborated from a simple standpoint of uniform growth which does not necessarily ever obtain in any living body.

II. The mathematical data corresponding to such a standpoint have been deduced and tabulated, in accordance with the simple numerical data afforded by plant phyllotaxis systems; and thus it has been shown that the divergence angles of such uniformly growing asymmetrical systems can be deduced mathematically, while by simple geometrical constructions very reliable results may be obtained by one quite ignorant of mathematics. Also, granting the reasonable hypothesis that the lateral members of a plant are formed in one growth-system controlled by the shoot-apex, the curves of the transverse components of such members for different systems have been deduced and figured.

III. Given these data, it now remains to take them to the plant and note how far confirmation of the theory of orthogonal construction can be obtained, as implying an orthogonal distribu-

---

* *New Phytologist*, 1902, p. 49 ; *Annals of Botany*, vol. xviii., p. 227.

tion of growth-energy comparable with that of the electro-magnetic field.

The curves plotted by Mr E. H. Hayes should thus represent the fundamental shape of the leaf-sections, and the general equation is definitely put forward as a mathematical definition of a "leaf" outgrowth.* Such curves, if seen in sections, would not at first be regarded as equivalent to circles, while closely packed members approach under similar conditions the form of quasi-squares; the conducting tissue (vascular bundles) being orientated around a point described as the centre of construction. With the help of these curves and data it now becomes possible to pass on to the next phase of growth and study the phenomena of varying rates of growth, and more especially the retarded growth-systems and unilateral modes of distribution which clearly characterise the growing-points of shoots and the formation of leaf-laminae as studied in planes other than the transverse, which has so far alone been considered.

* *Annals of Botany*, vol. xviii., p. 227.

NOTES AND ERRATA. (PART II.)

Page 92. Cones from the same two trees of *Pinus austriaca* and *P. laricio* have been counted by Mr E. G. Broome for 1902 with similar one-sided results.

Thus *P. Laricio* (1902) :—

1st	100	.	.	34	R. and 66	L.	
2nd	,,	.	.	32	,,	68	,,
3rd	,,	.	.	18	,,	82	,,
4th	,,	.		29	,,	71	,,
5th	,,	.	.	41	,,	59	,,
6th	,,	.	.	31	,,	69	,,

or an average of

69·16 L. and 30·83 R :

a result practically identical with that of the two preceding years for the same tree : the average for 1100 cones during the three years being

69·82 L. and 30·18 R.

Pinus austriaca (B.G.O. 1902).—A poor crop only admitted of 500 cones being counted :—

1st	100	.	.	54	R. and 46	L.	
2nd	,,		.	63	,,	37	,,
3rd	,,			54	,,	46	,,
4th	,,			58	,,	42	,,
5th	,,		.	41	,,	59	,,

the average being 54 R. and 46 L. The result again is sufficiently identical with that of 1901. It may be pointed out that two of these batches gave very widely different results, in one batch a preponderance of left-hand cones being found, a fact which serves to show that 100 is too small a number to give a satisfactory conclusion. The average result for 1600 cones during three years for this particular tree is thus

54·06 R. and 45·94 L.

Page 116. *Fibonacci Ratios.*—The relation of the sequence 2·1·2·1·2, etc., is not quite so definite as stated, the summation being correct up to 34 ; since 34 members of the series do not add up to 55 but 54 ; similarly, 55 members add up to 88.   To keep the ratio correct in an expansion system an extra curve must be put in : this does not affect the value of the convention, since the series must be arranged around a circle, and the sequence must be broken somewhere. Since a strict adherence to the 2·1·2·1·2 sequence would in these cases result in the formation of multijugate systems, this property of the numbers involved renders the accuracy with which the expansion ratios succeed one another still more remarkable.

Page 153, line 25, *for* 36, *read* 63.

Note on Dichotomous Systems in Helianthus annuus.

Dichotomy of the shoot-apex of the type described in *Lycopodium Selago* (fig. 79, II., III.), and found characteristically in the *Lycopodiaceae* and allied forms, is possibly to be regarded as the most primitive type of ramification of the main axis of aerial plants.   At any rate the causes which have directed the evolution of the axillary branching of the strict type met with in higher plants still remain far to seek, though there can be little doubt as to the biological utility of the method so widely adopted.   Dichotomy of such a strict type is less frequent among higher plants, and its occurrence would as a matter of fact be usually classed as a *monstrosity*.   It is clear, however, that such dichotomy, however anomalous it may be considered, represents the first step in the production of the still more complicated growth-systems included under the heading of *Fasciation*, and that the division of a growth-centre into *two equal centres* is the simplest case of irregularity.

Helianthus annuus, which has so frequently been taken as the most typical representative of phyllotaxis phenomena, owing to the marvellous accuracy of its inflorescence construction scheme, has already been shown to present in addition all the typical phenomena of symmetrical and asymmetrical constructions, the perfection of Fibonacci relationships, and also the peculiar relationships of bijugate construction : it again becomes a plant of special interest from the frequency of the occurrence of strict dichotomy, which in garden specimens may affect the whole of the lateral branch system of the plant. Similar phenomena, but in a less perfect manner, may be noticed in such allied forms as *H. rigidus* and *H. strumosus*, in their garden varieties.   In such cases the dichotomy may occur (I.) in the foliage region, giving long-stalked pairs of capitula ; (II.) close behind the involucral region, giving twin-heads ; and (III.) within the involucre, resulting in the phenomenon of "two-eyed" capitula with a more or less perfect ray series between the two disks.

Observation of such systems shows that the irregularities recorded for *Lycopodium Selago* (p. 207) also hold good for *Helianthus* ; there being thus no necessary connection between the distribution of the primordia of the secondary centres, either between themselves or between these and that of the ·   ·   ·

parent shoot before this segmentation of the growth-centre took place. That is to say, the "genetic-spiral" may work out as homodromous or heterodromous, and the two capitula may be true "twins," *i.e. images* one of the other, or they may not ; and the latter is possibly the commoner case.

When the systems are homodromous, in the long-stalked form (Case I.), the close agreement of the position of the foliage-leaves is readily checked ; the only variations being clearly due to the secondary unequal elongation of the different internodes. Where heterodromy occurs, the point of bifurcation will be associated with a pair of equal leaves close together. In the case of the capitula themselves, homodromy or heterodromy is readily checked by noticing the course of the long and short curves of the disk, though this is often rendered impossible owing to the addition of structural irregularities.

The fact that phenomena of dichotomy, identical with those obtaining normally in *Lycopodium*, should occur as anomalous constructions in such a plant as *Helianthus*, would thus appear to suggest, not so much the extreme antiquity of the dichotomous method, as that this represents an alternative system of ramification which is worked out equally thoroughly in accordance with certain definite mechanical laws ; and different plants have at different periods selected that method which in the long run proved most satisfactory to them. Thus *Helianthus*, like other Phanerogams, exhibits normally a system of axillary branches, but still retains the power to arrange an alternative method of construction, just as *L. Selago* is typically dichotomous in its assimilative region, but presents in addition a copious formation of true axillary shoots which are subsequently utilised as gemmae for a secondary biological purpose.