Fig. 1.

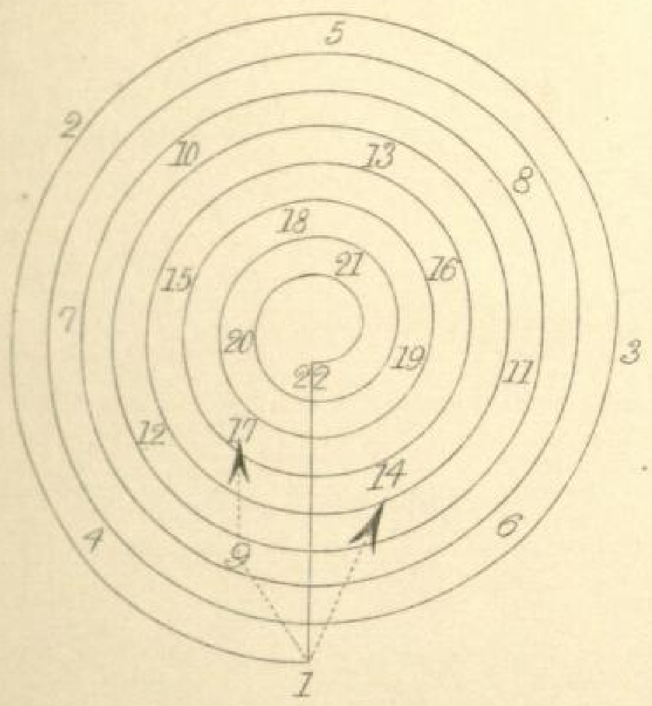


Fig. 2.

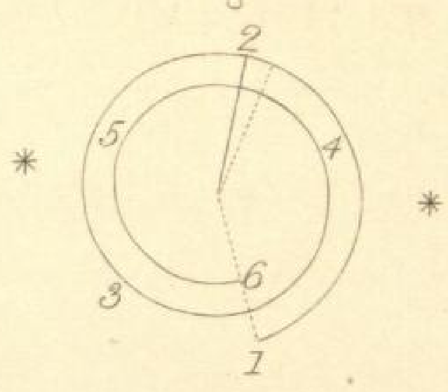


Fig. 3.

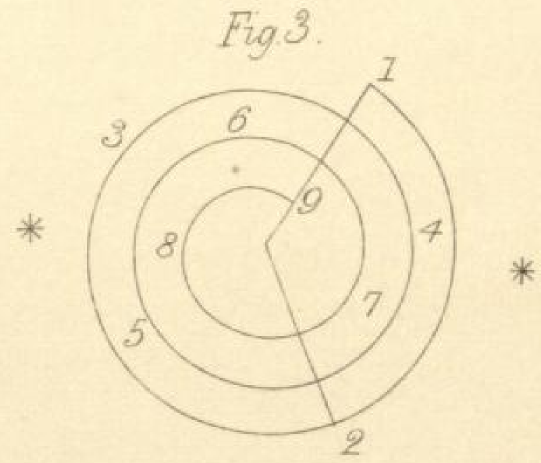


Fig. 4.

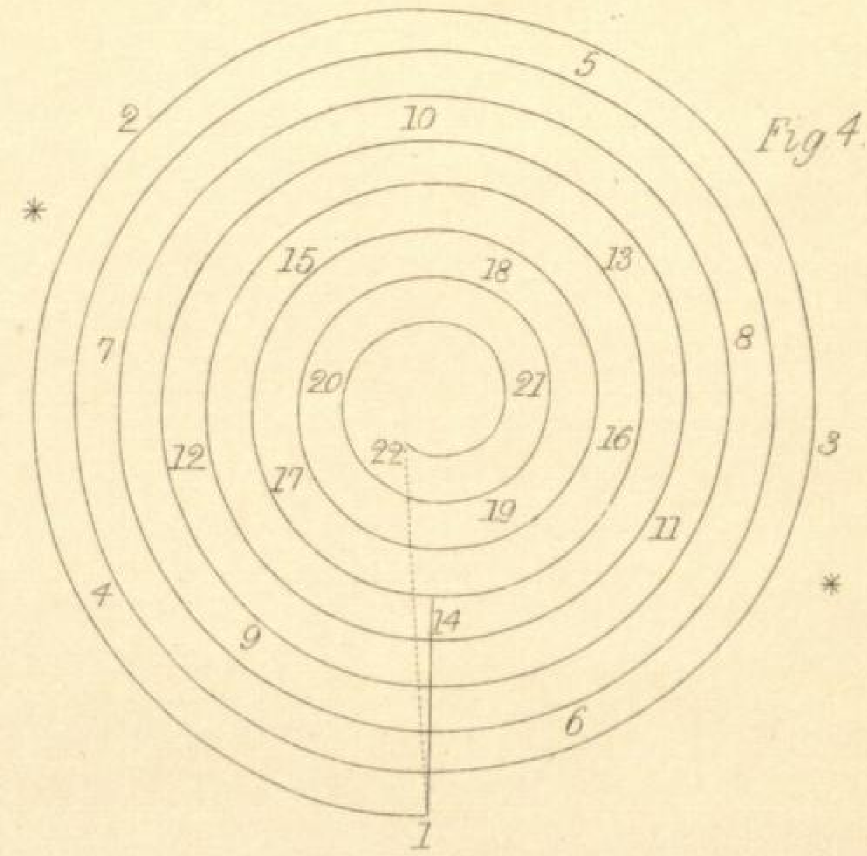


Fig. 5.

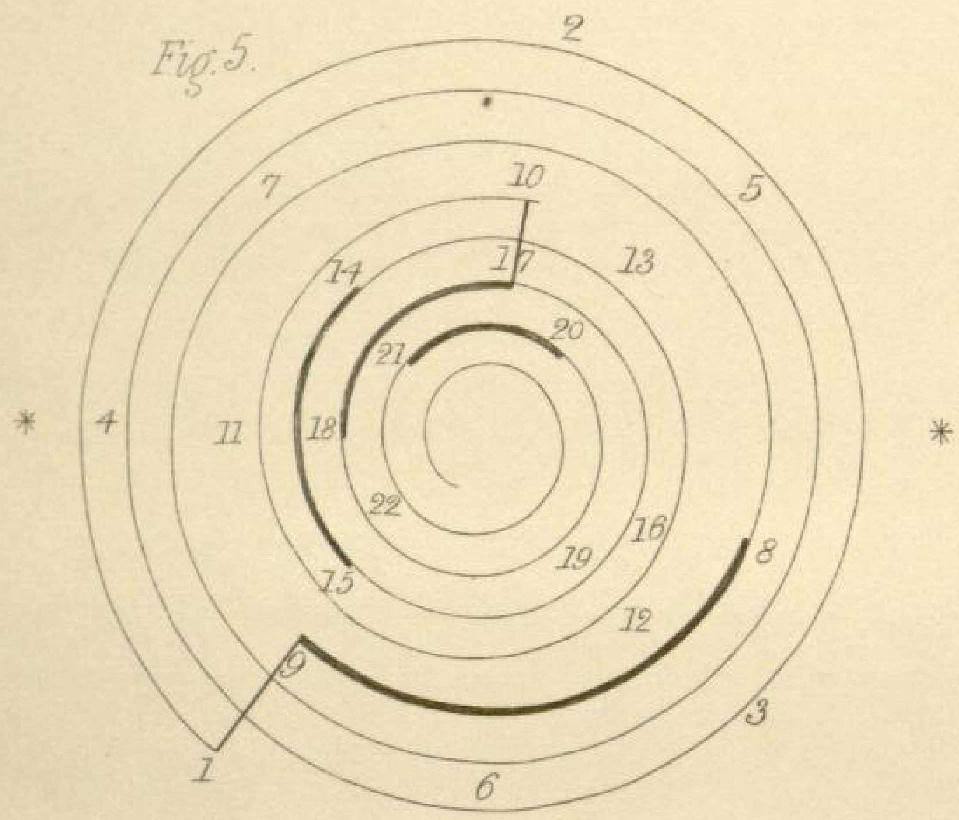


Fig. 6.

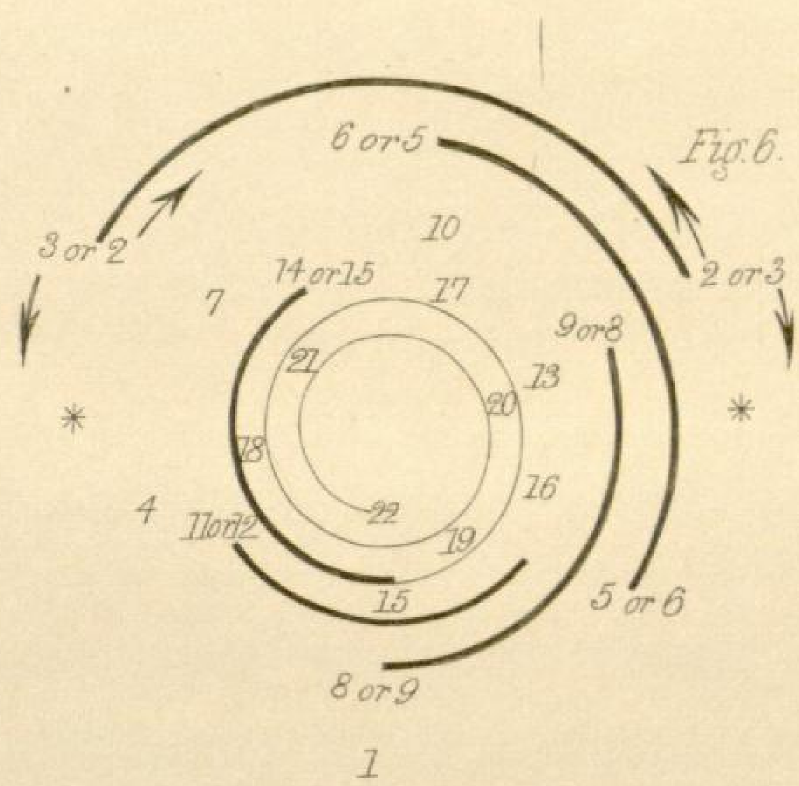


Fig. 7.

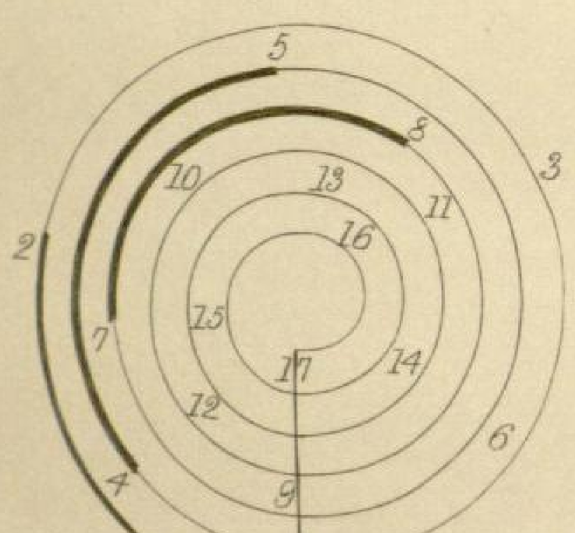


Fig. 8.

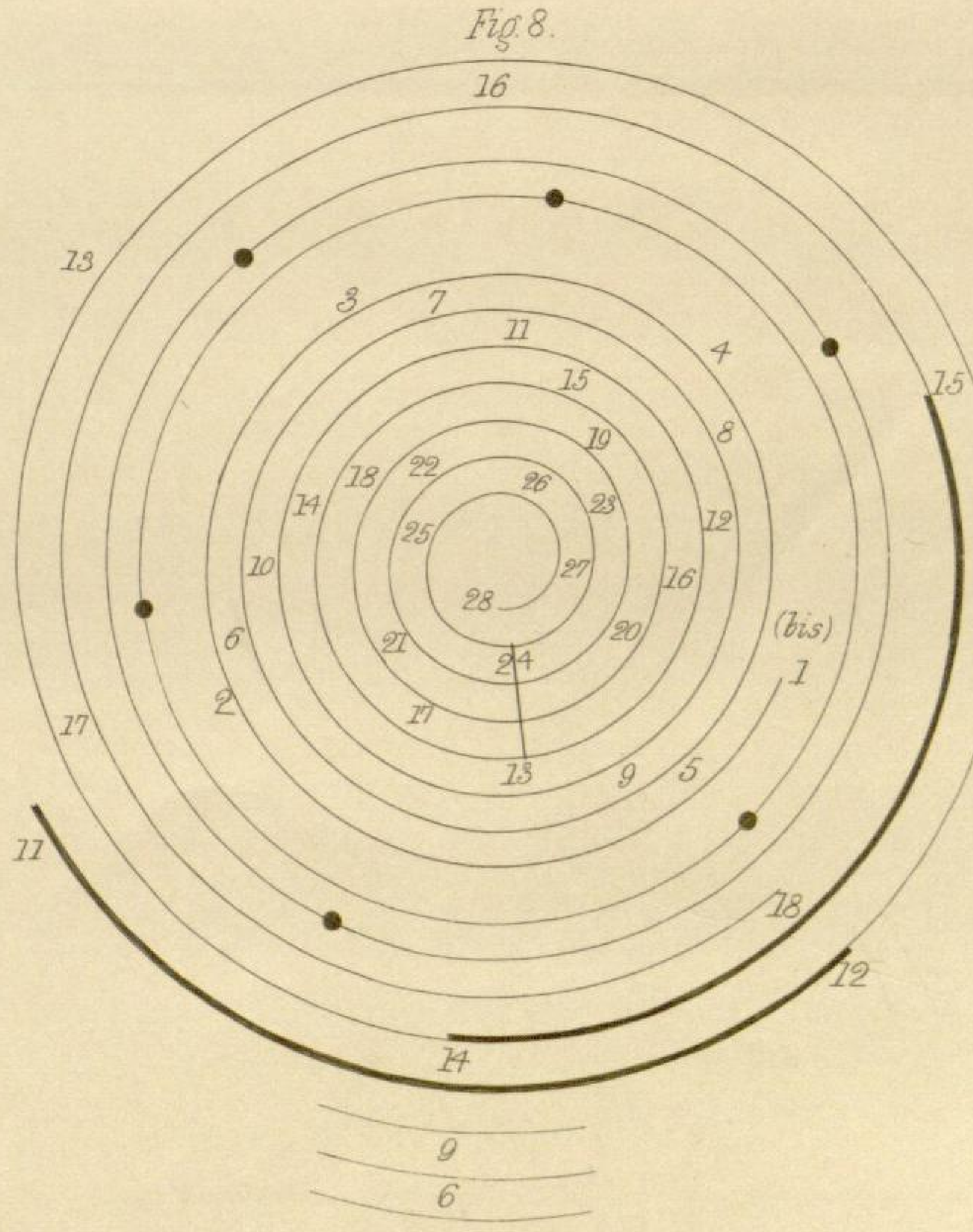
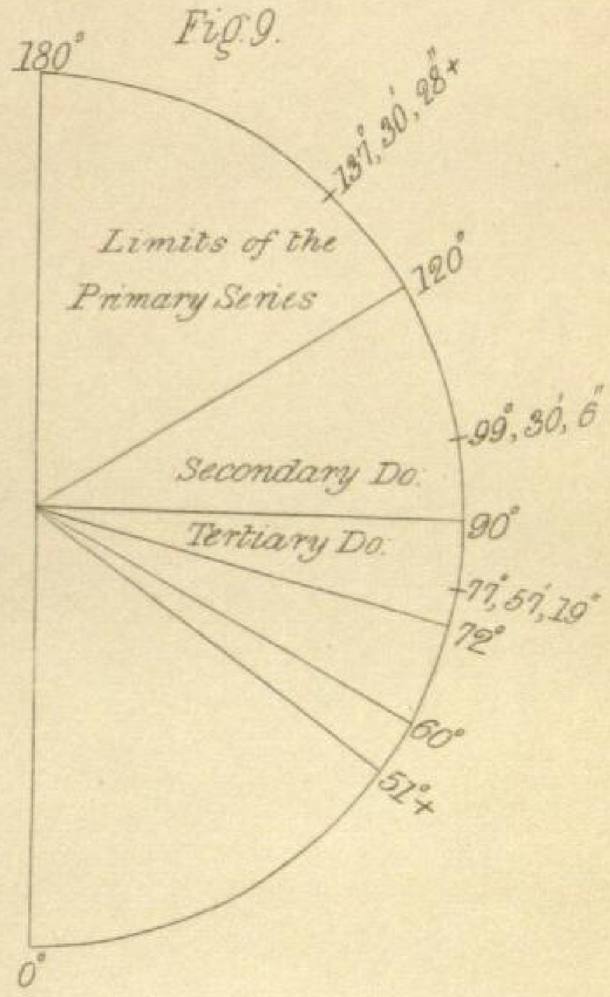


Fig. 9.



G. Henslow del.

G. Jarman sc.

XV. *On the Variations of the angular divergencies of the Leaves of* Helianthus tuberosus. *By the Rev.* GEORGE HENSLOW, *M.A., F.L.S.*

(Plate L.)

Read April 16th, 1868.

THE angular divergences of leaves and their homologous appendages, as represented by the different fractions of the well-known series, are for the most part tolerably constant; but it sometimes happens that in following the leaves spirally up a stem, we find vertically over the leaf selected as the first a different one from that which we should have expected. That cycle, therefore, must be represented by a different fraction to the one preceding.

Again, in continuing our observations from the point last reached, we find perhaps the same number of leaves after the same number of revolutions in the third cycle as in the first; or, on the other hand, the leaf in the same vertical line may be found only after an additional number of revolutions, and the cycle which ends at that point will accordingly be represented by a higher fraction of the series.

Again, if any number of stems on which the leaves are very numerous and their internodes short, or of cones on which the scales are very crowded, be taken, and we attempt to make out the angular divergences of their generating spirals, difficulties frequently arise—partly because the growth of the leaves or scales may not be exactly the same throughout, partly in consequence of some slight torsion of the axis, or from some unaccountable cause, independently of the fact that the generating spirals of cones very frequently belong to some curviserial form *; so that we may be at a loss to select the leaf or scale placed actually, or even nearly, vertically above the one selected below, especially as in many cases the spiral does not admit of strict verticality.

In examining the arrangements of the leaves on about eighty stems of the Jerusalem Artichoke, I found a very considerable amount of variation. The following divergencies were especially common:—

$\frac{2}{5}$ occurred on about	28	per cent.†	of the stems	examined.
$\frac{3}{8}$,, ,,	40	,,	,,	,,
$\frac{2}{7}$,, ,,	23	,,	,,	,,
A decussate arrangement	47	,,	,,	,,
$\frac{2}{5}$ throughout the stem . .	11	,,	,,	,,
$\frac{3}{8}$,, ,,	12	,,	,,	,,
A tricussate‡ arrangement	15	,,	,,	,,

* *Curviserial* divergences are those, for the most part, represented by the higher fractions of the series, *e.g.* $\frac{8}{21}$, $\frac{13}{34}$, &c., whose denominators are irrational, or no measure of the circumference.

† *i.e.* for one, two, or more cycles only.

‡ I adopt the word "tricussate" for whorls of three leaves each, in which the leaves of each whorl alternate with those of the whorls above and below it.

In endeavouring to trace the transitions which so frequently occurred in the stems from one kind of divergence to the other, I met with some which were new to me. Thus $\frac{2}{7}$ was, as given above, by no means uncommon; another was $\frac{3}{11}$; and occasionally an approximation to $\frac{1}{4}$ and $\frac{5}{18}$ appeared. Now these fractions can manifestly be arranged into a series analogous to the usual one, viz.:—

$$\frac{1}{4}, \frac{2}{7}, \frac{3}{11}, \frac{5}{18}, \text{\&c.};$$

where we see at once, by comparing them with

$$\frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \text{\&c.},$$

that while they retain the same numerators, the denominators of the successive fractions of this secondary series consist of the sum of the numerators and denominators of the corresponding fractions of the first or primary series, as I propose to call it.

I must here observe that the primary series arises from a fact which appears to be a very important one, and, as far as I am aware, has not hitherto been noticed, *i. e.* that every coil of the helix commencing with the position of any leaf, contains two other leaves beside the initial one. Thus, referring to fig. 1, if we start from leaf No. 1, No. 4 is not reached until after the coil has been completed, on arriving at the vertical line through the initial leaf; similarly, commencing with No. 4, No. 7 is found to be in the next coil; so that no such coil ever contains more than three leaves.

In the secondary series every such coil will contain four leaves. The same numerators are retained for the corresponding fractions of both series, as they represent the number of coils in each cycle, and they are not altered by the number of leaves being increased in each coil.

In a similar way it may be seen that tertiary, quaternary, and other series might be deduced, in which each coil will contain five, six, or more leaves successively. And, further, the following algebraical expressions will represent every series of divergence.

Let a be any number; then the fractions

$$\frac{1}{a}\quad \frac{1}{a+1}\quad \frac{2}{2a+1}\quad \frac{3}{3a+2}\quad \frac{5}{5a+3}\quad \frac{8}{8a+5}, \text{\&c.}$$

are quite general, and will include the angular divergences of all generating spirals.

They are based upon the principle that any portion of the spiral subtending 360°, *i. e.* a single coil of the helix as above described, contains $a+1$ leaves. To each series there is an initial fraction, viz., to the primary $\frac{1}{2}$, to the secondary $\frac{1}{3}$, to the tertiary $\frac{1}{4}$, &c., which must be exempted from the foregoing remarks, as the leaves in a projected coil of the spiral corresponding to these fractions are but two, three, four, &c., respectively. It will be hereafter shown how these initial fractions are the connecting links between the several systems or series of divergences *.

* Since discovering the existence of other series than the primary amongst the leaves of *Helianthus tuberosus*, and thence deducing the algebraical formulæ to represent all divergences, I have found, by referring to MM. Martin and Bravais's *résumé* of MM. Schimper and Braun's researches on Phyllotaxis (Ann. des Sc. Nat. 2me sér. vii. 1837), that much the same expressions have already been suggested from independent sources. It is, however, I think, interesting to find that a single species has so many variations of arrangement that it alone has afforded the means of arriving at very considerable generalizations.

On the Transitions from one kind of divergence to another of the same or of different series.

On referring to the diagram (fig. 1.) of the divergence $\frac{8}{21}$ of the primary series, it will be seen that in consequence of no projected coil, as described above, containing more than three leaves, the angular divergences of all the spirals of these series will necessarily lie between 120° and 180° inclusive, or those represented by $\frac{1}{3}$ or $\frac{1}{2}$, and particular numbers will arrange themselves right and left, and nearest to the assumed vertical line corresponding to any generating spiral. Thus, for the fraction $\frac{8}{21}$, two numbers in close proximity to this line, and situated below the 22nd leaf (which commences the second cycle), are the 9th and 14th. These, together with the initial leaf selected as No. 1 of the generating spiral, form the commencement of two secondary spirals through the numbers 1, 9, 17, 25, 33, 41, &c., and 1, 14, 27, 40, &c., the angular divergences of which, *as generating spirals*, would be represented by the fractions $\frac{3}{8}$ and $\frac{5}{13}$ respectively. Hence it can be seen that by shifting, as it were, the 22nd leaf to the one side or the other, some other leaf will fall exactly or approximately over the first, and the generating spiral will no longer be represented by $\frac{8}{21}$, but by some other fraction. And as the leaves nearest to the vertical line passing through the 1st and 22nd leaf are those which commence the second cycles of spirals, represented by fractions $\frac{5}{13}$ on the one hand, and $\frac{13}{34}$ on the other, these are found to be the divergencies into which $\frac{8}{21}$ would most readily pass.

Similarly, if a vertical line be drawn corresponding to the $\frac{5}{13}$ divergence, by a slight movement to the left (suppose), the 22nd leaf comes most nearly over the first, and the spiral arrangement of $\frac{8}{21}$ is obtained; but if a greater displacement to the right had taken place, the 9th leaf would have fallen over it; or, again, by a still greater displacement to the left, the sixth will be vertically over the first; and we thus pass into the arrangements for the generating spirals represented by the fractions $\frac{3}{8}$ and $\frac{2}{5}$ respectively.

Exactly analogous results can be obtained from the secondary and other series of fractions; for if we select the line passing through the 1st and 19th leaves, or the vertical line for the divergence $\frac{5}{18}$, we can, by supposing a slight deviation to the right, bring the 29th leaf over the 1st, so that the generating spiral would now become $\frac{8}{29}$. Likewise by a deviation to the left the 12th leaf would arrive over the first, and a transition be thus obtained into the divergence $\frac{3}{11}$; or, if we had first chosen the vertical for this arrangement, *i. e.* a line through the 1st and 12th leaves, then it is easy to see how a change can be effected, either into the lower members of the series $\frac{2}{7}$ or $\frac{1}{4}$, or to the higher one $\frac{5}{18}$.

Generalizing these remarks, it becomes clear that similar transitions can be presumed possible in all other series, and, further, that any one series can pass into another, provided it be represented by a generating spiral, the angular divergence of which is a low one in that series, *i. e.* either itself being one of the divergences $\frac{1}{3}$, $\frac{1}{4}$, $\frac{1}{5}$, $\frac{1}{6}$, &c., or capable of passing into one of them, as, from these, passages may be presumed possible from the primary into the secondary, secondary into tertiary, and *vice versâ* respectively, inasmuch as each of these fractions is common to two series.

On the Methods of ascertaining the Numerator and Denominator of Fractions representing generating spirals of all series.

In order to find the numerator and denominator of the fraction representing a generating spiral, where the leaves or scales are so crowded that it cannot be readily discovered by inspection alone, the usual rules are as follows:—Either to affix*, first of all, the proper numbers to each scale, and then observe that which falls upon the scale vertically over the first, and which, lessened by 1, gives the denominator; while, to find the numerator, the axis must be allowed to revolve, when the number of revolutions made in passing from No. 1 to the scale over it will give it. Or, if we take the common differences corresponding to the two secondary spirals which pass through the scale selected as No. 1, and also the scales *nearest to, but immediately below*, the scale vertically over the first, the sum of these common differences supplies the denominator, and the smaller of them the numerator.

The former of the two methods will apply to any spiral of any series. The latter rule, though of application in the primary, fails to give the *numerator* for any divergence other than those included in that series; but if it be remembered that the numerators are respectively the same for the corresponding fractions of every series, no great difficulty will be met with in affixing the right one to any denominator. This arises from the fact that the number of coils in a cycle is the same for all such fractions, the real difference being in the number of leaves in a coil. Thus $\frac{3}{8}$, $\frac{3}{11}$, $\frac{3}{14}$, are the third fractions in the primary, secondary, and tertiary series, in which each coil of a cycle has 3, 4, 5 leaves respectively.

The fact of each coil having the same number of leaves, whatever arrangement be taken (provided it be from one and the same series), appears to be a very important principle, and hitherto, I believe, overlooked. Yet it is mainly† upon this fact that all calculations are really based. That this is the case will be understood from the fact that if any spiral of the primary series, by a diminution of the angular divergence, were to possess four leaves in a single coil, it would become a member of the secondary series. Similarly, if a spiral of the secondary series shall possess five leaves in any of its coils, it will pass into the tertiary series.

On certain Relations between the Fractions of the several Numerical Series.

It has been already noticed that the sum of the numerator and denominator of any fraction in one series forms the denominator of the corresponding fraction in the next series; thus, if they be written down as follows,

Primary series . . . $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, $\frac{13}{34}$, &c.,
Secondary series . . $\frac{1}{3}$, $\frac{1}{4}$, $\frac{2}{7}$, $\frac{3}{11}$, $\frac{5}{18}$, $\frac{8}{29}$, $\frac{13}{47}$, &c.,
Tertiary series . . . $\frac{1}{4}$, $\frac{1}{5}$, $\frac{2}{9}$, $\frac{3}{14}$, $\frac{5}{23}$, $\frac{8}{37}$, $\frac{13}{60}$, &c.,

* It is assumed that the reader is familiar with the method usually given in elementary text-books.

† It must be remembered that as the position of any 2nd leaf of a spiral of the primary series has a range of 60° for its position, viz. from 120° to 180°, in other words, all angular divergences of that series lie between $\frac{1}{3}$ and $\frac{1}{2}$ inclusively, there must be some "innate guiding principle" (for want of a better expression till the cause be discovered) which gives these second leaves a tendency to stay at certain points within that range, and corresponding to the successive convergents of the primary series, the limiting point being at an angle of 137° 30′ 28″.

it will be at once seen that 5+2, or the sum of the denominator and numerator of the third fraction of the primary series supplies the denominator 7 to the third fraction of the secondary series, and so on.

Next, it may be observed that the same connexion which has been long noticed in the primary series holds good also for all others, viz., the sum of the denominators of any two adjacent fractions is the denominator of the next succeding, *e. g.* 7+11=18, &c.

Again, it has been noticed that in the primary series any numerator is the same number as the denominator of the fraction *next but one* preceding it. Now this relation cannot be maintained in any other series; but if it be remembered that the denominators can be formed by adding the numerator and denominator of the corresponding fraction of the preceding series, the true and general relation at once appears, as in the following examples:—

The denominator of the fraction $\frac{3}{8}$ supplies the numerator to the fraction $\frac{8}{21}$; but in the secondary series the denominator is 11(=8+3); so also in the tertiary series the denominator of the corresponding fraction is 14(=11+3=8+2×3). Hence it appears that the fourth fractions might be arranged as follows:—$\frac{3}{8}$, $\frac{3}{8+3}$, $\frac{3}{8+2\times 3}$, $\frac{3}{8+3\times 3}$, &c.

Generalizing from this observation, if $\frac{a}{b}$ represent any fraction of the primary series, $\frac{a}{b+a}$, $\frac{a}{b+2a}$, $\frac{a}{b+3a}$ will represent the corresponding fractions of the secondary, tertiary, and quaternary series respectively.

Lastly, MM. Schimper and Braun have shown that the fractions of these series are the successive convergents of the continued fractions $\frac{1}{2+}\ \frac{1}{1+}\ \frac{1}{1+}$ &c., $\frac{1}{3+}\ \frac{1}{1+}\ \frac{1}{1+}$ &c., $\frac{1}{4+}\ \frac{1}{1+}\ \frac{1}{1+}$ &c., the limiting values of which are represented by $\frac{3-\sqrt{5}}{2}$*, $\frac{5-\sqrt{5}}{10}$, $\frac{7-\sqrt{5}}{22}$, &c., respectively, which, when multiplied by 360°, give the angles 137° 30′ 28″, 99° 30′ 6″, 77° 57′ 19″ as the limiting angular divergences for the first three series respectively. [*Vide* Ann. des Sc. Nat. 2^{me} sér. vii. 1837.]

ILLUSTRATIONS OF THE TRANSITIONS FROM ONE DIVERGENCE TO ANOTHER AMONGST THE LEAVES OF HELIANTHUS TUBEROSUS.

I. *Transitions from the Decussate arrangement into Spirals of the Primary series.*

The stems, the leaves of which commence at the base in a decussate manner, had, on the average, seven pairs of opposite leaves placed alternately at right angles to each

* The method of obtaining this result will be understood from the following:—

$$\text{let } x=\frac{1}{1+}\ \frac{1}{1+}\ \frac{1}{1+}\ \text{\&c., and } y=\frac{1}{2+x};$$

from the equation $x=\frac{1}{1+x}$ we obtain $\frac{\sqrt{5}-1}{2}$ as the value of x,

$$\text{and therefore } y=\frac{2}{\sqrt{5}+3}=\frac{3-\sqrt{5}}{2}.$$

4 x 2

other; but above them the leaves gradually assumed some spiral form by *shifting* to the right or left (*i. e.* of the observer in front).

i. No instance of a direct change from opposite leaves into the $\frac{1}{3}$ arrangement presented itself; indeed, to accomplish this, the divergence would have had to pass from one limit to the other, *i. e.* from 180° to 120°.

ii. The change from the decussate into the $\frac{2}{5}$ divergence occurred not unfrequently. The method by which it was effected will be understood by reference to the diagram (fig. 2), in which it will be observed that the positions of the leaves numbered 1 and 2 are not strictly opposite, and that radii drawn from them to the centre do not pass at right angles to the diameter through the asterisks which indicate the position of the highest pair of opposite leaves; so that these radii include an angle of about 150°. Again, by a similar approximation of the 3rd and 4th, and of the 5th and 6th leaves, we find, on completing the second turn of the spiral, that the 6th leaf is over the first; so that a transition into the $\frac{2}{5}$ divergence has been established from this point.

It must be noted that the angles between the radii drawn from the centre through successive leaves of this first, and of what might be called *transitional* cycle, do not accurately equal 144° or $\frac{2}{5}\times360°$, as indicated by the dotted radii. But as the spiral arrangement is continued up the stem and into the terminal bud, the leaves seem to "right" themselves, as it were; so that the appearance of the spiral in the neighbourhood of the summit is more accurate than at the point of departure from the highest pair of opposite leaves.

iii. In a similar manner to the above, direct transitions into the $\frac{3}{8}$ arrangement occurred quite as often as into the $\frac{2}{5}$, the only difference being that the angle included between radii drawn to the pair of leaves which converge to one side is less than 150°, —indeed, nearly, if not quite accurately, 135°, which is the angular divergence of the $\frac{3}{8}$ arrangement.

iv. Only one instance occurred where opposite leaves were resolved in a similar way directly into the $\frac{5}{13}$. When this fraction was otherwise represented, it was due to a slight shifting of the leaves in the cycle following upon one or more preceding cycles of the $\frac{3}{8}$ divergence.

II. *Transitions from the Decussate arrangement into Spirals of the Secondary series.*

i. No instance of a direct transition from the decussate into the $\frac{1}{4}$ arrangement presented itself*.

* Although two pairs of decussate leaves are at right angles to each other, and therefore, if projected on a plane, have an angular divergence of 90°, or $\frac{1}{4}$, yet, if the internodes be developed, the order of the leaves could not be such as is required for the $\frac{1}{4}$ arrangement, but would be thus,—

```
      2
      5
 3 8     7 4
      6
      1
```

Although no such transition occurred with decussate leaves, this process was frequently illustrated in the breaking up of tricussate leaves, as will be shown hereafter.

ii. A transition from opposite leaves into the $\frac{2}{7}$ occurred in about 15 per cent of those stems commencing at the base with decussate leaves. It can apparently only be effected by some previous approximation to the "tricussate" grouping of leaves. The process will be best understood by referring to the diagram (fig. 5), which illustrates the actual position as observed in nature; in which it will be noticed that, from the 1st to the 9th leaf, the spiral is to the left, and that, in consequence of the 8th and 9th leaves becoming confluent, the latter is ranged over the first, while the 10th becomes nearly opposite and is over the second. From this point (the 10th leaf) the spiral turns to the right, and, by the 14th and 15th, the 17th and 18th, becoming confluent, the 17th leaf is over the 10th, and thus the $\frac{2}{7}$ arrangement is commenced, and henceforth continued uninterruptedly into the undeveloped terminal bud.

A more usual way, however, of passing from opposite leaves into the $\frac{2}{7}$ arrangement is by throwing out an extra leaf at right angles to the diameter passing through them (fig. 6), and by converging the first pair towards the opposite side, and in this manner exhibiting a tendency to produce a whorl of three leaves, and consequently four in any single coil commencing with the position of some leaf. A point to be observed in this method is, that if the confluent pair be exactly on the same level, either one may be taken as the second leaf of a cycle commencing with the first isolated leaf. Thus the 8th or 9th leaf will be immediately over the 1st, according as the spiral is chosen to one side or the other, corresponding to the divergences $\frac{2}{7}$ or $\frac{3}{8}$ respectively. The leaves of each confluent pair generally become isolated at last, one being elevated above the other, so that a true spiral is ultimately secured.

It must be observed that the same angular distance between the two confluent leaves answers for two kinds of spiral, viz. $\frac{2}{7}$ and $\frac{3}{8}$. This is of course, strictly speaking, impossible, as the angular divergence for $\frac{2}{7}$ is $102° 51' 77''+$, and for $\frac{3}{8}$, $135°$; but this condition is only transitional. When the leaves become isolated the proper angular divergence is subsequently secured, and is generally $\frac{2}{7}$.

iii. The next fraction of the secondary series is $\frac{3}{11}$. This was only occasionally represented, with a commencement of decussate leaves at the base of the stem, by a previous transition into the $\frac{2}{7}$ spiral—and by the "vertical" line passing through the 1st, 8th, and 15th leaves being itself really inclined, and so forming a secondary spiral, in consequence of which the 12th leaf falls approximately over the 1st.

iv. In like manner $\frac{5}{18}$ was occasionally reached by a passage through $\frac{3}{11}$ and $\frac{2}{7}$.

III. *Transitions from the Tricussate arrangement into Spirals of the Primary series.*

i. Three verticillate leaves were never resolved directly into the $\frac{1}{3}$ arrangement; yet in certain stages of change it occasionally happened that a 4th leaf would fall nearly over another selected as the 1st. Similarly no case appeared of a direct transition into the $\frac{2}{5}$ arrangement. Indeed it appears that tricussate verticils are more readily resolvable into spirals of the secondary series, just as decussate leaves are most readily convertible into those of the primary.

ii. The diagram (fig. 7) will illustrate the manner of transition from tricussate leaves into the $\frac{3}{8}$ divergence, a change which occurred in about 30 per cent. In this case the

3rd leaf is isolated; but the 2nd, though still confluent with the 1st (as indicated by the thickened line in the fig.), is slightly raised. Similarly the 5th, though united to the 4th by the broad base of the petiole, is at a slightly higher level. The same remark applies to the 8th; but the internode between the two confluent leaves, the 7th and 8th, is now much increased. Above the 8th the leaves are entirely free; and finally the 9th is vertically over the 1st, so that the $\frac{3}{8}$ divergence is established.

IV. *Transitions from the Tricussate arrangement into Spirals of the Secondary series.*

i. No direct change from tricussate into $\frac{1}{3}$ or $\frac{1}{4}$ occurred.

ii. A change from verticils of threes into the $\frac{2}{7}$ was frequent. It takes place in the following manner:—The 1st step is to cause the three leaves of the different whorls to separate slightly by a development of their internodes. Then, if any two consecutive whorls be examined, the order of succession of the six leaves (No. 1 being the lowest leaf) is thus,—

6
3 7 9 2
8
4 5

1

in which it will be noticed that the 4th leaf, instead of being over the interval between the 1st and 2nd, is over that between the 1st and 3rd; so that the angle between the 1st and 2nd leaves, or between the 2nd and 3rd, is *double* that between the 3rd and 4th. These latter, it will be remembered, are separated by a long internode. The same order obtains with the succeeding whorls; the nodes, however, are now much more widely separated, while a true spiral arrangement, with the same angular distance between all its leaves, is ultimately secured, and is henceforth continued uninterruptedly into the terminal bud, and represented by the fraction $\frac{2}{7}$.

Another method of separation of the three leaves of the whorls consists in one leaf only becoming isolated (as was the case in the transition from tricussate into $\frac{3}{8}$ divergence), while the other two remain coherent at the same level. The result obtained in this case, it will be remembered, is identical with that secured in certain cases of change from decussate leaves, where a *third* leaf is thrown out at right angles to the diameter passing through the supposed original positions of the opposite leaves, which now converge to one side. From this stage either of the two following results may occur:—On the one hand, by the ultimate separation of the two confluent leaves, the $\frac{2}{7}$ spiral is secured (as described in the case of the passage from decussate leaves into that divergence), or, on the other hand, the two confluent leaves may never separate at all, so that a repetition of two coherent and one single leaf occurs up the stem to its summit.

iii. Although the $\frac{2}{7}$ arrangement is by far the most general of the secondary series, as arising from the tricussate, yet other divergences occasionally occur with more or less accuracy. The diagram (fig. 8) illustrates a case in which $\frac{3}{11}$ commenced with the 18th leaf, in having the 24th almost accurately above it, which divergence was maintained henceforth uninterruptedly into the terminal band*.

* In the résumé of MM. Schimper and Braun's work on "Phyllotaxis," by MM. Bravais and Martin, these authors

V. *Transitions from Divergences of the Primary to those of the Secondary series.*

Transitions from one series to another upon the same stem do not appear to be readily effected. It rarely if ever occurs amongst the spirals of the *Helianthus* without some intermediate verticillate (either actual or approximate) arrangement.

If it be remembered, however, that for the primary series all divergences lie between 120° and 180° inclusively—for the secondary series, between 90° and 120°—and for the tertiary between 72° and 90°, it will be seen that to pass from the primary to the secondary the angle must be as near 120° as possible, or that represented by $\frac{1}{3}$. Now as this fraction is common both to the primary and secondary series, *we can conceive* of a passage from one series to another through that divergence. Similarly through $\frac{1}{4}$, or 90°, a passage could be effected from the secondary to the tertiary. Hence the series $\frac{1}{3}$, $\frac{1}{4}$, $\frac{1}{5}$, &c., would be the fractions indicating what might be called transitional divergences.

Such, however, was not the method obtaining amongst the leaves of *Helianthus tuberosus.*

The diagram (fig. 8) illustrates an instance where the leaves at the base of the stem were arranged for the first cycle according to the $\frac{2}{5}$ divergence (primary series) and revolving to the right. In consequence, however, of some misplacement in the second cycle, the 9th leaf fell over the 6th, *i. e.* the 1st leaf in that cycle, which must therefore be represented by $\frac{1}{3}$. In the third cycle there was a return to the $\frac{2}{5}$, as shown by the 14th leaf being over the 9th. In this cycle the 11th and 12th, as also the 14th and 15th in the next, became confluent, indicating therefore an attempt at a verticillate grouping. The 16th, 17th and 18th leaves were free, and, though distant about 120° from each other, were not at the same level. From this point a sudden change to two perfect whorls of three each occurred. Then a new spiral (of the secondary series) abruptly followed, revolving to the left, and containing four leaves in each coil, starting from No. 1 (*bis*). Of this spiral the first two leaves most nearly in the same vertical line were the 13th and 24th; and as there were three coils between them, the angular divergence now represented by the leaves was $\frac{3}{11}$. No further change occurred up the stem.

I may here mention that MM. Bravais and Martin observe that when transitions occur from one series to another, it is by nature selecting, as it were, for the change a new denominator as nearly the same as possible to the preceding; thus $\frac{3}{14}$ (in the tertiary series) may be followed by $\frac{5}{13}$ (in the secondary series). They, however, do not cite an example; and I would add that I met with no such instance; for in the *Helianthus* the change was almost invariably effected by an intermediate (either actual or approximate) verticillate arrangement.

The following examples will illustrate the principal cases of change from one kind of angular divergence to another on the same stem:—

notice the occurrence of changes from verticils to spirals and *vice versâ*. They state that if two different whorls have an intermediate spiral by which they are connected, then the fraction representing this spiral will be an arithmetic mean between the divergences of the whorls. Thus if a whorl represented by ($\frac{1}{6}$) be connected with a whorl of ($\frac{1}{5}$), the intermediate spiral will be known by $\frac{2}{11}$. They do not mention individual cases. (Ann. des Sc. Nat. 2me sér. viii. p. 170.) No such arrangement appeared amongst the leaves of the *Helianthus*.

I. Commencing with a decussate arrangement (D) at the base of the stem :—

1. D into $\frac{2}{5}$ into $\frac{3}{8}$ into $\frac{2}{5}$
2. „ „ $\pm\frac{2}{5}$* „ $\pm$T „ $\frac{2}{7}$
3. „ „ $\frac{3}{8}$ „ $\frac{2}{5}$
4. „ „ $\frac{3}{8}$ „ $\frac{2}{7}$
5. „ „ $\frac{3}{8}$ „ $\frac{2}{7}\pm\frac{1}{4}$ into $\frac{2}{7}$
6. „ „ $\pm\frac{3}{8}$ „ $\pm\frac{5}{13}$
7. „ „ $\frac{5}{13}$ „ $\frac{3}{8}$
8. „ „ (2+1)† „ $\frac{3}{8}$
9. „ „ (2+1) „ $\frac{2}{7}$

II. Commencing with a tricussate arrangement (T) at the base of the stem :—

1. T into $\frac{3}{8}$
2. „ „ $\pm\frac{1}{4}$ into $\frac{2}{7}$
3. „ „ $\frac{2}{7}$
4. „ „ $\frac{3}{11}$ into $\frac{2}{7}$
5. „ „ (2+1) „ $\frac{2}{7}$

III. Commencing with an alternate arrangement at the base of the stem :—

1. $\frac{1}{3}$ into $\frac{3}{8}$ into $\frac{5}{13}$ into $\frac{3}{8}$
2. $\frac{2}{3}$ „ $\frac{3}{8}$
3. $\frac{2}{5}$ „ $\frac{3}{8}$ „ $\frac{2}{5}$
4. $\frac{2}{5}$ „ (2+1)
5. $\frac{3}{8}$ „ (2+1)

Hypothetical Origin of the prevailing series.

By referring to the diagram (fig. 9) it will be seen that the angular distances included by the limiting positions of the second leaves of all generating spirals, commencing at 0, decrease according as the spirals belong to the secondary, tertiary, quaternary, &c. series; so also does the number of leaves in a single coil increase correspondingly; and therefore the higher the series the more nearly does any spiral belonging to it approach the verticillate condition, provided the internodes be but slightly developed. Now, if it be true that these higher series were more abundantly represented amongst "fossil vegetables," as M. Decandolle‡ remarks, or if, as Mr. Haughton§ says, the verticillate arrangements were universally represented, at least by the orders Filices, Equisetaceæ, and Lycopodiaceæ, then we can, I think, have some grounds for at least imagining such arrangements to have been the forerunners of spirals of the lower series, such as of the secondary and primary of the present day. But if we attempt to explain how such

* The symbol (±) indicates "approximately."

† (2+1) indicates the case of two confluent leaves together with one single leaf.

‡ "Théorie de l'Angle Unique en Phyllotaxie. Par M. C. DeCandolle" (Archives des Sciences Phys. et Nat. p. 14, 1865).

§ Manual of Geology. By Rev. Sam. Haughton, p. 245.

change came about, it can only be by mere speculation. We might, for instance, imagine that the crowded state of the leaves which must obtain where there is a comparatively large number in the same coil or circle might not be so advantageous to their development as a more scattered condition *. And hence we may be led to think that natural selection may have had some influence in bringing about these changes. We might be induced to speculate still further, and say that the verticillate, including opposite leaves, was the earliest arrangement, and that the spiral condition was a subsequent evolution; while the various changes of divergence of the Helianthus might remind us that it appears much easier to resolve verticils into spirals than to convert spirals into verticils. So, too, if analogy might be brought to bear upon this point, we might think that as "radial symmetry" (as we might call it) is characteristic of a lower organization amongst animals than the bilateral and integrated condition of organs belonging to those of a higher organization, so the multiplication of leaves and their more or less verticillate arrangement, might perhaps hint at an original truth, now well nigh obscured, if not obliterated by the evolution of ages. But putting all such speculations aside, no successful attempt has hitherto been made to ascertain the *cause* of any definite arrangement existing at all. We are quite as unable to explain it as to give a reason why the numbers 5 and 4 prevail among the parts of Dicotyledonous flowers, and 3 among those of Monocotyledons.

So, again, if we limit our inquiries to the condition of the primary series alone, we find, as a fact in nature, that if we assume any leaf as No. 1, then No. 2 lies between 120° and 180° inclusively, and that, too, either to the right or to the left. If we are asked why it is so, we can give no answer. Further, starting with this condition, we find that the position of this 2nd leaf is not *anywhere* along that arc, but that it has an inherent tendency to take up a definite point as its position; and, again, when we compare the positions of all such 2nd leaves in a variety of plants, or, as has been shown, in the *Helianthus tuberosus* alone, we find that the series of points between 120° and 180° affect an approach towards some limiting and intermediate point, which point, however, no known example has ever reached. If we ask, again, why the 2nd leaves endeavour to take up these definite positions and are not anywhere over the arc, there is as yet no answer to this question, any more than to the first. All that appears capable of exact statement is, that such are the conditions found to exist in nature, and that when the angles between the first and second leaves of all the different generating spirals are measured, and represented as fractional parts of the circumference, they are found to bear such relations to one another, when written down in succession, as obtain between the successive convergents of the continued fraction of the general form $\frac{1}{a+}\ \frac{1}{1+}\ \frac{1}{1+}\ \frac{1}{1+}$ &c.

* Perhaps the fact that in many cases where leaves occur either in a verticillate or fasciculate condition, they are not unfrequently more or less inclined to be linear or acicular in form, may give some countenance to this idea; such at least is the case in the following orders and genera:—Coniferæ, Galiaceæ, Equisetaceæ; Hippuris, Callitriche, and Myriophyllum. Conversely, we might imagine a more scattered condition favourable to a greater development of limb.

EXPLANATION OF THE PLATE.

TAB. L.

Fig. 1. Projection of the divergence $\frac{8}{21}$. The arrows indicate the secondary spirals, $\frac{5}{13}$ to the right, and $\frac{3}{8}$ to the left.

Obs. The numbers in each figure indicate the position of the leaves.

Fig. 2. This projection shows the method of passing from the decussate condition into the divergence $\frac{2}{5}$. The dotted lines give the true angle (144°) between the first two leaves for this divergence. The number 2 indicates the *actual* position of the second leaf.

Obs. The * * (as also in figs. 3, 4, 5, 6) show the position of the pair of opposite leaves immediately preceding the spiral arrangements.

Fig. 3. Illustration of the usual method of change from the decussate condition into the divergence $\frac{3}{8}$. This is effected, as also shown in fig. 2, by a convergence of two leaves to one side; but the angle at the centre between them is less than in the case of a change to the divergence $\frac{2}{5}$.

Fig. 4. Illustration of a change from the decussate condition into the divergence $\frac{5}{13}$ or $\frac{8}{21}$ approximately.

Obs. In these cases the divergences being irrational, and the 14th or 22nd leaf being at a considerable distance above the 1st, it is somewhat difficult to say which divergence might represent most nearly the generating spiral.

Fig. 5. Illustration of a change,—1st, from the decussate arrangement into the divergence $\frac{3}{8}$, the spiral turning to the left, and terminating with the 9th leaf; secondly, from the 10th leaf the spiral is reversed, is right-handed, and belongs to the divergence $\frac{2}{7}$.

Obs. The thickened portions of the spiral between the Nos. 8 and 9, 14 and 15, 17 and 18, 20 and 21, signify that the leaves corresponding to those pairs of numbers respectively cohere by the expanded base of their petioles. (The same occurs in figs. 6, 7, 8.)

Fig. 6. This diagram illustrates a case where a pair of leaves, above a previously decussate arrangement, have converged to one side. Their supposed original position is indicated by the * *. The bases of their petioles remain confluent. A third leaf (No. 1) is *thrown out* on the opposite side, all three being on the same horizontal plane. This process here occurs five times; subsequently the true spiral arrangement of the divergence $\frac{2}{7}$ is eliminated by the development of the internodes.

Obs. 1. As each group of three leaves is on one and the same plane, if the *odd* one be fixed upon as No. 1, it is optional which leaf is selected as No. 2. Hence, if the one to the right be taken as No. 2, the leaf immediately over the first will be No. 8; and the arrangement must be represented by $\frac{2}{7}$. But if the one to the left be chosen as No. 2, then the same leaf immediately over the first will be No. 9; and *this* arrangement must be represented by $\frac{3}{8}$.

Obs. 2. In some cases the ultimate spiral was never eliminated (see fig. 5), but the grouping (2+1), or two leaves united and one free, and all on the same horizontal plane, was continued uninterruptedly to the summit of the stem.

Fig. 7. Diagram to illustrate the change from the tricussate arrangement into the divergence $\frac{3}{8}$. The first three leaves of the spiral are nearly in their original position, the 1st and 2nd being slightly convergent and still coherent. The 4th and 5th, as also the 7th and 8th, likewise cohere respectively; but above the 8th the leaves become entirely free by the development of their internodes, and, the spiral being now eliminated, this arrangement is continued uninterruptedly into the terminal bud.

Fig. 8. This projection represents a case where the leaves commence (at the base of the stem) with the spiral arrangement $\frac{2}{5}$ *to the right*, but for one cycle only; so that the 6th leaf is over the 1st. The next cycle belongs to the divergence $\frac{1}{3}$, by the 9th leaf being over the 6th with one coil

only; but the 14th, after two coils, appearing in the same vertical line, there is a return to the divergence $\frac{2}{5}$. The 11th and 12th, as also the 14th and 15th, leaves cohere respectively. At the 18th leaf the spiral ceases. Then followed two whorls of three leaves each, as shown by the dots. A new spiral *to the left* next commences [from 1 (bis)]; and as the 24th is the first leaf which is found to fall as nearly vertical as possible over any one preceding (viz. 13th), and as there are three coils from 13th to the 24th, the divergence $\frac{3}{11}$ is established, and thenceforward continued upwards without further interruption.

Fig. 9. This diagram illustrates the limiting positions of leaves of spirals corresponding to divergences of the different series.

If 0° be the position of any leaf taken as the commencement of any spiral arrangement of the primary series, then the second leaf of that spiral will fall between 120° and 180° inclusively.

Similarly any second leaf of a spiral of the secondary series falls between 90° and 120° inclusively.

And of the tertiary series any second leaf will fall between 72° and 90°. In a like manner "limiting arcs," as they may be called, can be found for all higher series, which, it will be observed, decrease in size as the No. of the series increases.

The "limiting angle" to which all divergences of the primary series continuously approximate as they ascend that series is 137° 30′ 28″. The same for the secondary series is 99° 30′ 6″. The same for the tertiary series is 77° 57′ 19″.