

XI. *On the Origin of Floral Æstivations. With Notes on the Structure of the Cruciferous Flower, on that of Adoxa, and on the Corolla of Primula. By the Rev. G. HENSLOW, M.A., F.L.S., F.G.S.*

(Plate XXV.)

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INTRODUCTION.

THE idea of endeavouring to trace out any laws that may exist amongst floral æstivations arose in my mind from observing the large number of *diagrams* given in Le Maout and Decaisne's 'Descriptive and Analytical Botany,' in which the æstivations of about 250 genera of Dicotyledons and of 50 of Monocotyledons are diagrammatically expressed. I therefore proceeded to draw up an enumeration of all the different kinds, and to ascertain what percentage each had amongst the genera, and what connexions there might be amongst those different kinds. I then examined a number of living flowers of several genera, but soon found my work had been to some extent inefficient as based upon very insufficient data*.

So far from each diagram given being the sole example or even always typical of a genus, I found it to be the commonest thing for a species to have a very considerable amount of variation, as will be seen at the close of this paper. As an example, the diagram of *Primula*, p. 529 (Engl. ed.) †, is not the only kind, as this genus can boast of at least eight varieties in the Primrose alone. Again, the diagram of the male flower of *Hydrocharis*, p. 754, does not correspond with the figure of the flower given there, in that the inner whorl of the figure is "tristichous," while it is represented as "convolute" in the diagram. Lastly, two diagrams of *Hermannia* are given on p. 284, as if it were an unusual occurrence for a flower to have its whorls running spirally in opposite directions, whereas it is an extremely common occurrence. Hence, if any one should be led to imagine these diagrams to be in all cases characteristic or the sole kinds of æstivation peculiar to each genus respectively, he will be much mistaken. It may be observed, however, that nothing is said respecting them whatever, as to whether they *do* represent typical forms or not. On the other hand, the æstivations of many genera are remarkably constant, such as the universally "convolute to the left" corolla of *Myosotis*; or again, the valvate calyx with contorted corolla of Mallow, though even here the "imbrication" may be either to the right or left; and when this is the case, it may become, as Robert Brown pointed out, a valuable diagnostic character.

* The draught of this paper was made on recovering from a long illness, when I had but few opportunities of testing the conclusions given from the study of the diagrams alone. I, however, give these conclusions, because the reader will be able to refer to the diagrams in that excellent work, and because the deductions made from a comparison of those diagrams is generally very similar to that derived from the examination of the variations in the flower-buds of living plants.

† The references to *pages* throughout this paper always refer to Le Maout and Decaisne's work.

Little attention, indeed, appears to have been paid to æstivations until that eminent botanist called attention to their importance*. Since then nearly all text-books describe the principal forms, but without tracing any or but slight connexions between them.

If we turn to our latest authorities, we find Le Maout and Decaisne, for example, devoting two pages (86, 87) to the subject in describing, as usual, the different kinds, and also attempting to explain the "papilionaceous" and "cochlear" by, as I believe, a wrong application of the "quincunx;" while in Sachs's 'Text-book of Botany,' "æstivation," "imbricate," "contorted," and "valvate," are words conspicuous by their absence from the index as well as from the text. Many diagrams occur in that work; but the subject of æstivation seems to have been totally ignored.

The laws of phyllotaxis have to some extent been adapted to the floral whorls, more especially and obviously to the quincuncial or $\frac{2}{5}$ plan. The very frequent occurrence of this latter amongst sepals and petals is of itself a sufficient indication that phyllotactical laws are in certain cases applicable—as also the fact that the outer whorls of flowers are in some cases composed of many parts and spirally arranged, especially when there is no manifest "break" between the whorls, as in *Calycanthus*, *Cactus*, &c. In these cases the $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, and even $\frac{8}{21}$ arrangements may be detected.

II. THE FORMS OF ÆSTIVATION,

The following include those usually described, as well as one or two in addition.

1. *Distichous equitant*, or the $\frac{1}{2}$ arrangement in which one of the two opposite parts overlaps the edges of the other, as in *Papaver* (Tab. XXV. fig. 1).

The *half-equant* is a modification of this, in which one edge of each part overlaps one of the edges of the other part respectively, as in the calyx of Poppy and the corolla of *Circæa* (Tab. XXV. fig. 2).

2. *Tristichous* or the $\frac{1}{3}$ arrangement. This is especially characteristic of Monocotyledons. It may be observed that it is identical with the "imbricate proper" when the whorl has only three parts, so that the first overlaps the second, and the latter overlaps the third, which last also underlies, with its opposite edge, the first (Tab. XXV. fig. 3).

3. *Pentastichous*, *quincuncial* or $\frac{2}{5}$ arrangement, in which the parts of the whorl correspond with those of one projected "cycle" of that plan (Tab. XXV. fig. 4).

4. *Half-imbricate*.—I apply this term to a large number of instances ranging from complete regularity to such extremely irregular forms as the corollas of the Violet, the Pea, and the Snapdragon. It is produced by a slight modification of the quincuncial—namely, by the edge of the second part being overlapped by instead of itself overlapping the fourth part (Tab. XXV. fig. 5).

5. *Imbricate proper*†, in which the parts of a whorl overlap each other in succession,

* A short summary of the history of the nomenclature of æstivations has lately appeared from the pen of Prof. A. Gray, in the American Journal of Sciences and Arts, vol. x. Nov. 1875, and is reprinted in the Journal of Botany, new series, vol. v. p. 53.

† I call this "imbricate proper," as the word "imbricate" is also used technically for an indefinite number of parts, as in the scales of *Calycanthus* &c., which overlap like tiles on a roof. Linnæus appears to have included all these forms (viz. 3, 4, 5, and 6) under this term (see Prof. Gray's paper l. c.).

so that one, the first, is entirely outside the adjacent parts, while the last is entirely within. This is deduced from the last by allowing the third member to slip one edge under the fifth, in addition to the second being under the fourth (Tab. XXV. fig. 6).

6. *Convolute and contorted*.—In these each part of the whorl overlaps one adjacent part by one of its edges, and is in turn overlapped by the other adjacent part (Tab. XXV. fig. 7). This is deduced from the preceding in a similar manner to that—namely, by passing an edge of the first part under that of the third.

Hence it will be seen that Nos. 3, 4, 5, and 6 are closely connected, and may be briefly expressed by saying the half-imbricate is formed from the quincuncial by having the 4th member over the 2nd, the imbricate proper from the half-imbricate, by having the 4th over the 2nd and the 5th over the 3rd, the convolute from the imbricate proper by having the 4th over the 2nd, the 5th over the 3rd, and the 3rd over the 1st*.

7. *Valvate*.—In this the edges of adjacent parts touch only, but do not overlap. The two main varieties, besides the simply valvate, where the edges just touch, are:—

Induplicative, where the edges are rolled inwards; *reduplicative*, where the edges are rolled outwards.

8. *Straight or open*.—In this the parts of the whorl are not sufficiently developed to meet even as in valvate, and therefore the æstivation may be said to be indeterminate.

III. THE DEGREES OF FREQUENCY OF THE VARIOUS KINDS OF ÆSTIVATION.

The following percentages are deduced from Le Maout and Decaisne, as stated above.

I. Dicotyledonous Angiosperms.

A. IMBRICATIVE.

| | | |
|---|--------------|---------|
| 1. Equitant Calyx | occurs about | 4 p. c. |
| „ Corolla | „ | 12 „ |
| 2. Tristichous, Calyx, or Corolla . . . | „ | 11 „ |
| 3. Pentastichous, Calyx, with Cor. various | „ | 24 „ |
| „ Corolla, with Calyx „ | „ | 10 „ |
| „ both Calyx and Corolla | „ | 14 „ |
| 4. Half-imbricate (excluding Papilionaceous and cochleate varieties) . . | „ | 15 „ |
| 5. Imbricate proper, Calyx, apparently very rare, as in <i>Cyclamen</i> , p. 529. | | |
| Imbricate proper, Corolla | „ | 9 „ |
| 6. Convolute, Calyx, apparently rare. | | |
| „ Corolla | „ | 16 „ |

* Prof. A. Gray's paper is chiefly directed to the settlement of the proper term for this kind; and he concludes that "convolute" is preferable to "contorted," as the latter does not differentiate corollas with a torsion, the petals of which have each a spiral axis, from those with no torsion, or whose axis is erect. A third term, "obvolute," would, he observes, claim priority as having been used by Linnæus; but it has not been in common usage. As the Professor concludes with the words, "I should hope rather than immediately expect that this use would become general," I have the satisfaction of fulfilling those expectations immediately; for although this paper was written before Prof. Gray's was published here, and I had adopted the word "contorted," I have altered it in every case to "convolute," in accordance with his wish.

B. VALVATIVE.

7. Valvate (including varieties).
 Calyx valvate, with Corolla various . occurs about 11 p. c.
 Corolla valvate, with Calyx various . „ 6 „
 8. Straight or open.
 Calyx open, with Corolla various . „ 28 „
 Corolla open, with Calyx various . „ 5 „

II. Petaloid Monocotyledons.

1. Equitant is represented in 3 genera
 only besides Grasses.
 2. Tristichous, outer perianth whorl . . „ 40 „
 „ inner perianth whorl . . „ 60 „
 3. Pentastichous occurs in *Paris polyphylla*, p. 859.
 6. Convolute, represented in 4 genera only.
 7. Valvate „ 20 „
 8. Open „ 30 „

IV. REMARKS ON THE PRECEDING VARIETIES OF ÆSTIVATION.

1. *Equitant*.—The proportion of flowers which have equitant whorls, either entirely, when one member of the pair is embraced by both the edges of the opposite member, or half-equantant, in which each of the pair overlaps one edge of the other, occurs in corollas about 12 p. c. and in calyces about 4 p. c., as calculated from the diagrams of Le Maout and Decaisne. Probably this is not far from being correct.

With regard to the origin of this kind, I am inclined to think it is due to a reduction of parts from the tristichous or pentastichous arrangements, and in some cases may be a retention of a primitive condition. If one member of a tristichous whorl be suppressed, the other two will most probably become equitant, as flowers almost* invariably arrange their members either radially or bilaterally symmetrically. Such, I suspect, will account for this æstivation in poppies, for example, where the calyx is half-equantant and the corolla equitant (Tab. XXV. fig. 1). *Papaver* and its nearest allies of the tribe *Eupapavereæ* are usually binary or quaternary in their perianths, though whorls of threes are not wanting, and seem to point to their ancestral character, which is retained in *Romneyæ*. Moreover *Papaver orientale* not unfrequently develops a third smaller sepal, which may or may not be accompanied by a trimerous corolla, which I take to be due to atavism.

If this theory be correct, the ancestors of poppies were trimerous; but by the arrest of one part in the calycine and one in each of the corolline whorls, these have become dimerous and equitant in æstivation.

* There are a few rare instances, due to insect agency, such as *Polygala chamaebuxus* and *Phaseolus*, which are, so to say, “distorted.” I use the word *symmetrical* here in its popular, not botanical sense, as usually restricted, though Sachs applies it thus. The term *zygomorphic* has been used to express bilateral symmetry, and, if generally adopted, would avoid much confusion.

Or again, if we start with a quincuncial arrangement, the equitant condition is arrived at by suppressing either the first or fifth member. This, I think, has probably been the case with *Actæa* (p. 186) and *Adoxa* * (p. 474), as well as with the *Cruciferae* †. *Circea* (Tab. XXV. fig. 2), however, I am inclined to think owes its equitant æstivation either to an original dimerous symmetry derived from opposite leaves, or else it may be due to "symmetrical reduction" from a tetramerous type which prevails in the same order (*Onagraceæ*) to which it belongs.

If the equitant æstivation is presumably derived from a quincuncial whorl of five parts, by the arrest of one, the four remaining will probably be wholly equitant at first; but they may undergo further changes. If it be the result of a convolute æstivation, then the remaining pairs will more likely be half-equantant. Thus, if *Circea* be derived from a tetramerous type with convolute petals, as occurs in *Epilobium*, by the arrest of two opposite parts, then it will be seen how each part of the remaining pair will overlap the other reciprocally, and the resulting æstivation will become half-equantant (Tab. XXV. fig. 2).

I would not, however, venture to lay very much stress on this supposed difference in the origin of half-equantant as compared with equitant whorls; for the overlapping of another by the edge of any part may be simply due to some slight advantage in growth quite irrespective of any cause arising from antecedent conditions—as, indeed, may be the case with the calyx of *Papaver*, which is half-equantant, though, as I presume, its dimerous character is derived from a tertiary type.

2. *Tristichous*.—This will be seen to be identical with an imbricate-proper æstivation when the whorl consists of three members only. It is very common in the perianth-leaves of Monocotyledons, occurring in the outer whorl about 40 p. c., and in the inner whorl about 60 p. c., as deduced from the diagrams of Le Maout and Decaisne. This possibly would require some modification; for I found the convolute æstivation also very common, as in about one third of the flowers of *Crocus* examined. This kind is represented by those authors as occurring in only four genera. In a pound of dates I found the percentage of the inner whorl of the perianth as tristichous to be 82, and as convolute 18. The outer whorl is gamophyllous, and reveals no succession of parts.

The origin of the prevailing ternary arrangement in Monocotyledons I take to be simply due to the fact that it does *not* arise out of opposite leaves, which latter, as I have shown elsewhere, gives rise chiefly to the pentastichous arrangement (Trans. Linn. Soc. sec. ser. vol. i. p. 37), so common in Dicotyledons; hence, as the usual phyllotactical requirements demand three leaves for every projected circle, and the floral requirements demand an alternation of position in the successive whorls, so by these two effects there issues the usual alternation of groups of threes.

In Dicotyledons there is a group of orders with a ternary arrangement prevailing amongst them (*Magnoliaceæ*, *Anonaceæ*, *Menispermaceæ*, *Berberidaceæ*), associated with a few genera or orders having a large number of imbricated parts in their floral whorls (*Dilleniaceæ*, *Calycanthaceæ*, *Nymphæaceæ*, &c.). When the whorls are in

* See Note B, p. 194, on the variations of the symmetry of the flowers of *Adoxa*.

† See Note A, p. 191, on the origin of the arrangement of the parts of a cruciferous flower.

threes in these orders, I believe it to arise as just stated, and as is more fully explained further on (Note C, p. 194) from phyllotactical considerations; that is, a prolonged spiral, instead of furnishing whorls corresponding to cycles, as in *Aconitum*, is simply broken up into decussating whorls of threes.

3. *Pentastichous or Quincuncial*.—This arrangement is one in which the parts of a whorl constitute one cycle of that leaf-order. Each successive member is at an angular distance of 144° from the next in order. It appears to be the commonest in Dicotyledons, obtaining either in one, two, or more whorls of a flower, and, from the diagrams of Le Maout and Decaisne, occurs about 50 p. c. This deduction is quite corroborated by observations on individual plants; for in the flowers *e.g.* of Primrose* (which shows eight if not more varieties of æstivation) the pentastichous was about 40 p. c. Similarly is it with *Viburnum tinus*.

What I have said upon the origin of alternate leaf-arrangements in my paper referred to above, fully accounts for this plan being the commonest among Dicotyledonous Angiosperms. Indeed I would venture to call it one of the fundamental plans, as giving rise to at least three others, if not more, such as the half-imbricate, imbricate proper, convolute, and possibly in part the equitant.

4. *Half-imbricate*.—I apply this term to a very common arrangement, which does not appear to have been at all recognized before, but which is nevertheless a very important type of æstivation. It is deduced from the pentastichous by the 2nd member of that kind having one of its edges passing under the 4th, and is not only the first step towards the imbricate proper, and thence to the convolute, but will also explain the æstivation of many irregular flowers, such as the “papilionaceous,” that of the *Cæsalpineæ*, and the “cochlear”†, which, too, can be thus accounted for by a simpler method than is usually applied, and moreover a perfectly natural one, as it exists abundantly amongst floral whorls.

In the percentages deduced from the diagrams of Le Maout and Decaisne, that of this kind does not appear very high (16 p. c.). An examination of many flowers leads one to think it should be somewhat higher, as, *e.g.*, in *Laurustinus* it amounts to nearly 80 p. c., though in the Primrose it is certainly rare; similarly in *Ribes* it only amounts to about 10 p. c.

With regard to the papilionaceous corolla, if we consider the standard as No. 1, one of the keel-petals as No. 2 (of a quincunx), *which now passes under the wing, i. e.* No. 4, the wing on the opposite side of the median line will be No. 3, while the remaining keel-petal will be No. 5, coherent with No. 2.

* The diagram given by Le Maout and Decaisne of the Cowslip (miscalled Primrose), on p. 529, has both the calyx and corolla according to the imbricate-proper æstivation, and not pentastichous, which is much the most characteristic form. See Note D, p. 195.

Since this paper was sent to press, my attention has been called to Dr. A. W. Eichler's ‘Blüthendiagramme,’ in which he observes that this form is found both in regular and irregular flowers, and he gives a diagram of it for *Adowa*, p. 270, and *Valeriana officinalis*, p. 275; but he retains the name “cochlear.” This I purposely avoided, as it has only a specific and not generic value.

† In the translation of Le Maout and Decaisne the word “cochleate” is used instead of “cochlear,” which is the correct term: the former is descriptive of a spiral shell, and would be applicable to the coiled legume of *Medicago*.

Le Maout and Decaisne endeavour to explain the structure differently, by conceiving No. 1 to be one of the wings, No. 2 the other wing, No. 3 a keel-petal, No. 4 the standard, and the remaining keel-petal No. 5. They thus derive it from the quincunx by removing the standard from being entirely *within* to a position entirely *without* the rest (fig. 466, p. 87). Similarly with regard to the æstivation of the *Cæsalpineæ* as represented by the diagrams of *Cassia* and *Cercis* (p. 367), though in these some confusion in the explanation is made by those authors; for in describing (on p. 87) these diagrams, they say,—“The standard retains its normal position [*i. e.* within the others], and the quincunx is properly formed.” But in reference to the diagrams given in p. 367, this is clearly not the case. Both in that of *Cercis* and that of *Cassia*, if we take the outermost of the two anterior petals as No. 1, then No. 2 (whether the spiral be supposed to turn to the right, as in *Cassia*, or to the left, as in *Cercis*) is in neither case external also, as it ought to be for a quincuncial or pentastichous arrangement. If, however, we take, as I propose, the exterior anterior petal as No. 1, then the internal petal as No. 5, both the above kinds fall under this type, which I call half-imbricate.

It will be seen that No. 1 is not the same petal in both the papilionaceous corolla and that of these two genera of *Cæsalpineæ*. That this difference is of no relative importance will be shown hereafter. It may be remarked here, however, with regard to the standard not being identical with the fifth (internal) petal of *Cassia*, that the wings of the former lie over the keel, while in the latter genus it is just the reverse. This would seem to show that the papilionaceous resemblance is apparent only and not real.

The calyx in *Cassia* is represented as quincuncial, that of *Cercis* “open” and therefore indeterminate.

I recommend this interpretation as doing far less violence to the fundamental quincunx than that hitherto suggested; in other words, it is acquired by a simple alteration of position of *one edge only* of one petal. It may be observed, too, that it is obtained by regarding the parts of the spiral as running in the reverse direction to that according to the former method of regarding it.

This type of æstivation will also account for the so-called “cochlear,” as of the Snapdragon (Tab. XXV. fig. 10, and Le M. & D. fig. 468, p. 87, in which the numbers there given should be exchanged respectively as follows, viz. 1, 5, 4, 3, 2 should be written instead of 1, 2, 3, 4, 5). Thus by retaining the innermost (anterior) petal as No. 5, and by merely shifting No. 2 partially under No. 4, we obtain the æstivation as illustrated by the diagram.

Another illustration of the half-imbricate in connexion with the quincuncial will be found in the diagrams of *Scrophularineæ*. The calyx of *Scrophularia* (p. 585) is strictly quincuncial: the exterior sepal, No. 1, is posterior*; but if this be compared first with the diagram of *Linaria* (p. 584), it will be seen that the 2nd sepal (the right anterior) now passes under the 4th (or the right), the spiral being right-handed†; and the æstivation of the calyx is therefore half-imbricate. It is similar to the calyx of *Paulownia* (p. 584); only this spiral is left-handed. But now comparing these with the calyx in the

* The diagram is wrongly placed. The left-hand exterior sepal is the posterior one in reality.

† On the distinction between right- and left-handed spirals, see below, note, p. 186.

diagram of Snap-dragon, p. 583, the 1st sepal is no longer the posterior one but the left anterior; the spiral is left-handed; and the posterior sepal is the 5th, and completely within the others. The corollas of all three genera have the same æstivation, and are constructed on this plan, which I call half-imbricate, having, at least most commonly, the 5th petal as the anterior one.

It is rare to find any other part than the 5th in the anterior position of the zygomorphic whorl, when its æstivation is half-imbricate. There is, however, one case figured by Le Maout and Decaisne, viz. the diagram of *Streptocarpus* (p. 598), in which the 4th petal is the anterior one. It is also thus in *Azalea* and *Rhododendron*, in which the 5th petal (always the single petal, which is entirely within the others) is the posterior one. Lastly, in *Pelargonium* alone all these arrangements may be found.

The above shows that no necessity can be seen for No. 1 of a whorl being always the same in position and therefore always homologous.

I have already remarked that this arrangement furnishes conditions varying from perfect regularity in the whorls to extremely irregular ones. A few references to the pages of Le Maout and Decaisne will illustrate this.

1. Corollas regular or very slightly irregular:—

Pittosporum, p. 248; *Rue*, p. 317; *Parnassia*, p. 403; *Elder*, 481.

2. Corollas partially or decidedly irregular:—

Moringa, p. 235; *Dictamnus*, p. 316; Horsechestnut, p. 357; *Cassia*, p. 367; *Rhododendron*, p. 516; *Henbane*, p. 578; *Vitex*, p. 615.

3. Very irregular corollas:—

Pansy, p. 241; *Lathyrus*, p. 369; Snapdragon, p. 87; *Lamium*, p. 620.

Irregular and zygomorphic flowers are sometimes produced without any departure from the quincunx; for it should be observed that both the quincuncial and the half-imbricate æstivations can be divided symmetrically into two similar halves (as represented in Tab. XXV. figs. 4 and 5) by median lines. Thus is it with *Polygala* (Tab. XXV. fig. 11), which somewhat resembles the papilionaceous; but the æstivation is simply quincuncial and without any modification. Similarly amongst gamopetalous corollas the diagrams given of *Alloplectus*, p. 597, as well as that of *Achimenes*, p. 596, and *Adhatoda*, p. 606, though possessing irregular bilateral flowers, have yet their petals arranged on the quincuncial plan.

Irregular flowers with a quincuncial æstivation would seem to be comparatively rare; and when it does occur the various parts are not always homologous. Thus in *Ramondia*, p. 600, *Alloplectus*, p. 597, and *Achimenes*, p. 596, it is in the 4th part, while in *Stilbe*, p. 613, it is in the 3rd part, and in *Myoporum*, p. 610, it is in the 1st part, which respectively occupy the anterior position.

5. *Imbricate proper*.—In this æstivation the parts of the whorl may be three in number, as in the tristichous; four, as in *Holly*, p. 339, and *Euonymus*, p. 342; or more commonly five or more. The parts overlap one another in succession, so that the first is wholly exterior, and the 'last' (which is really the third of the original quincunx from which it is derived) is entirely within the spiral. Le Maout and Decaisne number the parts in succession, fig. 463, p. 86; but this is not, nor can it possibly be correct, at least in accordance with phyllotactical principles; for if it were, we should have *five* parts

in a single projected coil or circle, which can only arise from the series $\frac{1}{4}$, $\frac{1}{5}$, $\frac{2}{9}$, $\frac{3}{14}$, &c. I observe Prof. Gray also notices the mistake of those authors, which occurs also in other text-books. If, however, we proceed from the last-mentioned æstivation, or the half-imbricate, in which the 2nd part lies under the 4th, and place the 3rd under the 5th, we at once obtain the present kind.

In the percentages deduced from the diagrams of Le Maout and Decaisne, it will be seen that this kind is much less common (only 9 p. c.) than the preceding; and what appears true for genera is also true for flowers of individual plants. Thus Laurustinus and Primrose give the percentage of imbricate proper as only 10.

6. *Convolute*.—As the last is derived from the half-imbricate, so this is obtained from the imbricate proper, by placing the 1st part under the 3rd of the quincunx; so that if we write the connexion of these three kinds successively, it will appear as follows:—starting with the quincunx, if we place the edge of No. 2 under No. 4, we obtain the half-imbricate; next, place the edge of No. 3 under No. 5, and we get the imbricate proper; and lastly, in addition to these, place the edge of No. 1 under No. 3, and the convolute is secured.

As long as the convoluted petals are erect and their median lines vertical there will be no torsion; but in some cases the apex appears as if it were artificially twisted, as in Mallow, Flax, &c. In these cases the word “contorted” can be applied either with or without “convolute” as well.

In turning to the percentages deduced from the diagrams of Le Maout and Decaisne, it appears that in corollas of different genera the number recorded gives the convolute variety a position of 16 p. c.; and in comparing this with the percentages of the same kind, deduced from flowers of the same species, as of the Primrose, it amounts to 15 p. c., or almost the same.

7. *Valvate*.—Of this kind of æstivation, with its two varieties induplicative and reduplicative, little need be said. They are comparatively rare both among sepals and petals. With regard to the origin of it, I believe, in possibly the majority of instances, it is due to a degradation from the imbricative kinds, using that term in a general sense. It is at least probable in all instances where the flower is presumably due to a spiral phyllotaxis. The diagram of *Geum*, p. 382, appears to afford an instance of a transition from the quincuncial to the induplicative in the petals, while the calyx has assumed a reduplicative form. I have reproduced this diagram in Tab. XXV. fig. 13.

In some cases where the flowers are dimerous or tetramerous, a symmetry which has probably risen from a similar opposition in the foliage-leaves*, it is also probable that no spiral arrangement has ever intervened. This may explain the fact of *Clematis* being nearly the sole genus (*Naravelia* is properly a subgenus only) of *Ranunculaceæ* which has opposite leaves and tetramerous flowers with a valvate calyx. Similar is it with the genera of *Oleaceæ*, as the Lilac, the sepals of *Epilobium*, of *Rhizophora*, &c. An illus-

* I hope to develop this idea on a future occasion. I would just call attention to the significant fact that of the genera of *Rosaceæ*, comprising 71 in all, as recorded in the ‘Genera Plantarum’ (Benth. and Hook.), three only have opposite leaves, and these three are alone characterized as having tetramerous flowers, viz. *Rhodotypos*, *Eucryphia*, *Coleogyne*.

tration of opposite foliage-leaves coalescing in venation in a valvate manner is seen in some species of shrubby *Veronica*.

Of course there are instances of a valvate calyx accompanied by an alternate arrangement in the foliage-leaves, such as *Malva*. These, as also all "open" kinds of æstivation, may be and probably are due to degradation, in consequence of which the parts only grow just sufficiently large to meet in the former case but not overlap, or else, as in the latter instances, to fall short of one another altogether, as in the *Umbelliferae*.

V. REVERSAL OF THE SPIRAL.

A peculiar feature to be noticed is the frequent reversal of the direction in which the parts of successive whorls run, whether of the corolla in being different from the calyx, or the inner whorl of a monochlamydeous perianth from the outer. Of the 35 diagrams in Le Maout and Decaisne which have both calyx and corolla quincuncial, two have the calyx right-handed and the corolla left-handed. On the other hand, four have the calyx left-handed, while the petals form a right-handed spiral. All the rest have the calyx and corolla either right-handed or left-handed together*.

In examining several flowers of the same species, as in other matters, so in reversal, I found many single kinds of plants furnishing this phenomenon, as *Crocus* and *Malva sylvestris*, in which the right-handed and left-handed contortions were in equal proportions numerically.

VI. THE NUMERICAL ORDER OF THE PARTS OF WHORLS.

In examining the 34 instances of dicotyledonous Angiosperms, where both calyx and corolla are arranged on the quincuncial plan, the first petal of the corolla was found to be in 13 instances between the 1st and 3rd sepals; in 11 instances between the 1st and 4th sepals; and in 1 instance between the 5th and 3rd sepals. In all these cases the imaginary spiral line would be in the same direction, though not continuous from the 5th sepal to the 1st petal.

In 9 instances the spiral has to be *retraced* to discover the 1st petal. Of these latter in 3 instances the 1st petal lies between the 5th and the 2nd sepal, and in 6 instances

* With regard to the direction of the spiral, I always signify as *right-handed* the parts of a whorl the sections of which, as represented by a diagram, overlap on the right side, as *seen from the centre*, i. e. corresponding with the movement of the hands of a watch. I find this method more convenient for *diagrams* than the reverse, which is employed in the terms *sinistrorse* and *dextrorse* for spiral climbers. In that case it is more convenient to regard the spectator as being on the outside of the climber. Prof. A. Gray (*l. c.*) says:—"I note with satisfaction that Bentham and Hooker use these terms to signify from left to right or from right to left of a person supposed to stand outside of a closed bud, which is surely the natural position of the observer." This is without doubt perfectly true *for a bud*, but it is not *for a diagram*, which is a transverse section of a bud. In this case it is "natural" for the eye to rest on the centre. People invariably regard the hands of a watch as going from left to right; yet if instead of regarding yourself in the middle of the watch, you remember that you are outside of it, then the hands go from right to left when passing from 3 to 9 o'clock.

There appears to be some confusion in Le Maout and Decaisne's work; for they describe their diagrams, p. 80, of phyllotaxis as left-handed, though they are really right-handed if traced from the periphery to the centre; yet the descriptions of the two convolute corollas of *Hermannia*, p. 284, correspond to the method I have adopted; compare also the diagram of *Dianthus*, p. 256, which, again, is contrary to the latter, and is left-handed, though described in the text as right-handed.

between the 2nd and 4th; but in no instance amongst the diagrams given does it pass beyond two sepals. Lastly, in 7 instances, as stated above, the spiral of the corolla was completely reversed in direction from that of the calyx.

Similarly in turning to Monocotyledons we find, of the two whorls of the perianth, that some genera have both revolving the same way, others have one whorl the reverse of the other. Moreover the point where the second whorl begins in either case is as variable as in Dicotyledons. Thus, of those genera where both whorls revolve in the same direction, *Pinanga*, p. 812, and *Commelyna*, p. 568, commence the inner whorl with their 1st part between the 2nd and 3rd leaves of the outer whorl, both being right-handed spirals. In *Juncus*, p. 864, *Phormium*, p. 844, *Lapageria*, p. 856, and *Alisma*, p. 800—all being left-handed spirals—the 1st leaf of the inner whorl lies between the 1st and 2nd of the outer.

Again, in *Colchicum*, p. 850, *Fritillaria*, p. 843, while both whorls revolve to the right, the inner commences with its 1st leaf between the 3rd and the 1st of the outer. In *Butomus*, p. 798, Snowflake, p. 786, and *Toffieldia*, p. 851, the inner whorl commences diametrically opposite to the last leaf of the outer (that is, it lies between the 1st and 2nd leaf of that whorl), and moreover is in these three reversed in its spiral direction. In *Asparagus*, p. 859, the 1st leaf of the inner whorl lies between the 2nd and 3rd; while, lastly, in *Tradescantia*, p. 868, and the Pineapple, p. 766, it lies between the 1st and 3rd.

These statements clearly show that there is no single law causing a similarity of order in every case. On the contrary, the two whorls seem most capriciously arranged, the only common character being that in all flowers of two whorls to their perianth these should have their members alternating in position.

The preceding having been deduced from the diagrams of genera, I examined several species, and found that such variations as are here represented in different genera could be all illustrated by the flowers of a single species, as of the Snowdrop, Crocus, &c. I, however, retain the above paragraphs as referring to the diagrams, which will therefore furnish the reader with abundant illustrations.

VII. ON THE CAUSES WHICH DETERMINE THE VARIOUS KINDS OF ÆSTIVATION.

1. *Regular flowers*.—If the parts of a whorl are all on the same plane, it appears to be quite uncertain as to which member of the whorl shall be developed as the first or outermost, and that, if a calyx or corolla be both quincuncial, although theoretically their members are spirally arranged, yet practically No. 1 of the corolla may be any one of the five petals, and by no means necessarily as near to 144° as possible from the fifth sepal. This may be due to the fact that as the internodes are suppressed the nourishment is not only equally distributed over the circumference of the receptacle, but nearly or quite as equally in *time*, so that it is, so to say, a mere chance which part of a whorl gets the first start. Some slight differential impulse seems to occur with the first five kinds of æstivation; but with the convolute, valvate, and open no member can be called the first at all.

As in a single whorl the order of development of its parts is not always in accordance with the theoretically spiral arrangement, and still less is there any connexion between the

whorls by a continuous spiral growth, so also, in the order of development of the whorls themselves, it is by no means always true that they appear in succession acropetally.

Thus, as a consequence of a flower always terminating an axis, it is the fact that not infrequently there is subsequent intercalation of whorls exterior to some already formed. Thus in *Sileneæ* "the first whorl of stamens which appears is opposite the sepals, while the second is produced opposite the petals, and (according to M. Chatin, but my own observations scarcely corroborate the statement) *exterior* to the first-produced whorls"*. As far, however, as *Stellaria holostea* is concerned, the stamens opposite the petals seem to me to be intercalated *between* the first-formed stamens; so that the andrœcium forms one circle only. The petals, however, are decidedly later than both sets of stamens, the latter having attained considerable dimensions when the former consists of minute semi-circular plates. This subsequent intercalation of whorls is perhaps due to what one may call "developmental energy" being stopped in its axial course, and, thus diverted, evincing itself by lateral or lower outgrowths. This also helps to explain the acrofulgal order of expansion in *Adoxa* (see Note B, p. 194).

2. *Irregular flowers*.—There is, at least, a presumable probability, based upon what is known regarding the mutual adaptation of flowers to insects, that all irregular flowers have originally arisen by such adaptations, and that the varieties called "peloria" are reversions to the regularity of the primitive type†. Now, in order to become irregular, one obvious process is the greater development of one or more parts of a whorl, often at the expense of the others, which remain more or less dwarfed; so that it would be presumable *à priori* that irregularity would determine which part or parts should arise first from the receptacle. But this does not always appear to be the case, though at present I am not aware that any law has been discovered which regulates the order of growth. The fact that any adult part is larger than another part does not necessarily imply that it *started* first. Thus is it often with those anthers which appear first, and far outstrip the petals in size, as in *Stellaria*; yet the petals, when adult, often exceed the stamens immensely, as in the last-named genus and many others. A like remark may be made with reference to stipules of trees, as of the beech, which in the bud grow to four times the size of the leaf to which they belong, yet soon cease to grow, when the leaf ultimately exceeds them many hundred times.

M. Chatin (*l.c.*) also observes that the polystemonous andrœcia of *Mesembryanthemum*, *Opuntia*, *Cactus*, &c. are developed centrifugally; but the inner, older members become partially arrested, and the outer are the first to dehisce their anthers.

* "Some *Alsineæ*," that author observes, "with reduced flowers, give rise only to the whorl opposite the sepals. This is the rule in *Paronychiaceæ*, where sometimes the abortion of the stamens opposite to the petals is accompanied by the abortion of the petals themselves" (Bull. de la Soc. Bot. de France, C, 1874, p. 133). *A propos* of this fact, I would observe that these and other reduced flowers are mostly, if not all, self-fertilizing; and besides the degradation of the petals, as being no longer required for attracting insects, the number of stamens gets reduced, or more or less aborted; thus is it in *Senebiera didyma*, *Stellaria media*, *Viola canina*, and other species with cleistogamous flowers; sometimes the andrœcium is even barren, as in some early-developed individuals of *Capsella Bursa-pastoris*, *Glechoma hederacea*, &c.

† The order of "emergence" of the whorls of *Linaria vulgaris* is as follows—calyx, corolla (which is quite regular and spurless at first), stamens, and, lastly, the pistil.

In *Lamium album*, as illustrated by 'Sachs's Text Book,' p. 480, although 3 sepals appear before the other two, yet the adult calyx is scarcely irregular. On the other hand, the 5 petals appear together as equal-sized papillæ; the two posterior soon far outstrip the others, then arching over them protect the anthers even from a very young condition. The anterior petal in the adult stage is two-lobed, and might give rise to the impression that the lip was composed of two parts, whereas the history of its development reveals the fact that it is really single, while the "hood" is double. This is also corroborated by the fact that two vascular bundles run side by side between the two posterior and shorter stamens. In *Ajuga reptans* a converse process takes place, in that the posterior pair of petals soon become arrested, and the lip now grows rapidly, arches over, and protects the andrœcium just as the hood does in *Lamium*.

VIII. VARIETIES OF ÆSTIVATION IN THE SAME SPECIES OF DIFFERENT GENERA
RESPECTIVELY.

RANUNCULUS BULBOSUS, or Bulbous Ranunculus.

| | |
|-----------------------------|-------------------------|
| Quincuncial to the right. | Occurred about 22 p. c. |
| " " " left | " " 16 " |
| Half-imbricate " right | " " 6 " |
| " " " left | " " 8 " |
| Imbricate proper " right | " " 18 " |
| " " " left | " " 14 " |
| Convolute " " right | " " 8 " |
| " " " left | " " 4 " |

Anomalous:—Corollas having 6, 7, or 8 petals variously folded, but with a general tendency to be convolute; also a few with 5 petals, but abnormally imbricated.

VIBURNUM TINUS, or Laurustinus. On a corymb, with 125 flower-buds.

| | |
|-----------------------------|-------------------------|
| Quincuncial to the right. | Occurred about 23 p. c. |
| " " " left | " " 24 " |
| Half-imbricate " right | " " 12 " |
| " " " left | " " 26 " |
| Imbricate proper " right | " " 6 " |
| " " " left | " " 6 " |

Anomalous:—Corollas with 6 petals, three instances; with 4 petals, one instance.

PRIMULA VULGARIS, or Primrose. Of 120 flower-buds examined.

| | |
|-----------------------------|-------------------------|
| Quincuncial to the right. | Occurred about 22 p. c. |
| " " " left | " " 27 " |
| Half-imbricate " right | " " 4 examples. |
| " " " left | " " 4 " |
| Imbricate proper " right | " " 5 p. c. |
| " " " left | " " 6 " |

Convolute to the right. Occurred about 12 p. c.
 „ „ „ left „ „ 17 „

Anomalous:—Two instances with corolla 4-merous; two with 2 exterior petals, and 3 convolute within; one with 1 exterior and 4 convolute, one with 6 sub-half-imbricate petals.

RIBES COCCINEUM, or Crimson Currant.

Quincuncial to the right. Occurred about 50 p. c.
 „ „ „ left „ „ 33 „
 Half-imbricate „ right „ „ 6 „
 „ „ „ left „ „ 6 „
 Imbricate proper „ right „ „ 6 „

FUCHSIA COCCINEA.

Convolute to the left. Occurred about 67 p. c.
 Imbricate proper „ „ „ 27 „

Anomalous:—1 petal exterior, 1 interior, and 2 opposite and equitant—of this, two examples; one example with six petals, 8 corrugated sepals, 6 stamens, and 4 carpels.

CHEIRANTHUS CHEIRI, or Wallflower. The corollas of this plant afford a great variety of æstivations. The chief kinds are as follow:—

Imbricate-proper to the right. Occurs about 12 p. c.
 „ „ „ left „ „ 14 „
 Convolute „ „ right „ „ 14 „
 „ „ „ left „ „ 6 „
 Anomalous:—1 petal exterior with 3 convolute „ „ 12 „
 Modifications of equitant 37 „

GALANTHUS NIVALIS, or Snowdrop. Of 24 buds there were no less than 14 different ways of arrangement and order together.

In the following representations the outer whorl and numerical order are indicated by the upper figures, the inner whorl and the corresponding numerical order of its parts by the lower row of figures.

A. Examples of reversal of the spiral in the inner whorl as compared with the outer.

R. 1 2 3 } Convolute to R. } L. 3 2 1 } L. 3 2 1 } Convolute to L. }
 L. 2 1 3 } L. 3 2 1 } R. 1 2 3 } R. 2 3 1 } R. 1 2 3 }

B. Examples of both whorls being right-handed:—

1 2 3 } 1 2 3 } 1 2 3 }
 2 3 1 } 1 2 3 } 2 3 1 }

C. Examples of both whorls being left-handed:—

3 2 1 } 3 2 1 } 3 2 1 }
 2 1 3 } 1 3 2 } convolute. }

D. Anomalous :—1 leaf external, the other 2 equitant.

CROCUS.

A. Examples of the reversal of spiral in the inner whorl as compared with the outer.

$$\begin{array}{cccc} \text{R. } 1 & 2 & 3 & \} \\ \text{L. } & 3 & 2 & 1 \} \end{array} \quad \begin{array}{cccc} \text{R. } 1 & 2 & 3 & \} \\ \text{L. } 3 & 2 & 1 & \} \end{array} \quad \begin{array}{cccc} \text{R. } 1 & 2 & 3 & \} \\ \text{L. } 2 & 1 & 3 & \} \end{array}$$

$$\begin{array}{cccc} \text{L. } 3 & 2 & 1 & \} \\ \text{R. } & 2 & 3 & 1 \} \end{array} \quad \begin{array}{cccc} \text{L. } 3 & 2 & 1 & \} \\ \text{R. } 1 & 2 & 3 & \} \end{array}$$

B. Example of both whorls being right-handed,

$$\begin{array}{cccc} 1 & 2 & 3 & \} \\ & 2 & 3 & 1 \} \end{array}$$

C. Examples of both whorls being left-handed.

$$\begin{array}{cccc} 3 & 2 & 1 & \} \\ & 3 & 2 & 1 \} \end{array} \quad \begin{array}{cccc} 3 & 2 & 1 & \} \\ & 2 & 1 & 3 \} \end{array}$$

D. Both whorls convolute to the right.

E. Outer whorl imbricate proper, inner convolute. Sometimes both to the right, and sometimes both whorls to the left.

IX. Note A.—ON THE SYMMETRY OF A CRUCIFEROUS FLOWER.

It has been customary hitherto to refer the structure of a cruciferous flower to a binary or quaternary type, though in different ways*. But, seeing that the leaves are so generally pentastichous, I would suggest a reference to an original quinary arrangement, with a subsequent symmetrical reduction by the arrest of the fifth member of each whorl; by which it will be seen that the relative positions of the organs as they occur in a cruciferous flower can readily, but of course theoretically, be accounted for. Thus, if the sepals be supposed to be arranged quincuncially, then the external position of the the anterior and posterior sepals will immediately follow, these being numbers 1 and 2 of quincunx. (Compare the figs. 13 and 16 of Tab. XXV.) Next, assuming the 1st of the five petals to lie between the 1st and 4th sepal (for the whorls must alternate), and the 1st of an outer whorl of five stamens to lie between the 1st and 4th petals, we shall have the 1st and 2nd retained as stamens (forming the two exterior lateral and lower ones), and the 3rd and 4th (opposite the anterior and posterior sepals) arrested or represented by glands.

The next whorl of stamens arising in a similar manner, it will be seen how the 1st and 4th will form, by approximation, one pair, the posterior, and the 2nd and 3rd the other pair. Lastly, the pistil is probably composed, as has been often suggested, of four carpels; but their union, according to my hypothesis, would be as follows. The two posterior carpels, numbers 1 and 4, coalesce to form the posterior half of the pistil, while the 2nd and 3rd, uniting in front, will form the anterior half. Thus two coherent

* A summary of the various theories may be found in Le Maout and Decaisne's 'Botany,' pp. 229, 230. See also "Note sur une monstruosité de la fleur du Violier (*Cheiranthus Cheiri*, L.)," par M. P. Duchartre, Ann. des Sc. Nat., 5^{me} série, xiii. p. 315.

margins give rise to the posterior placentas as well as the stigma opposite to them (this latter being composed of two adjacent marginal and coherent stigmas). Similarly the two anterior margins of the 2nd and 3rd carpels will give rise to the anterior placentas, with *their* combined stigmas. The four lateral margins I conceive as cohering down the middle of the valves; but their placentas and ovules are usually arrested. The stigmas, however, of these lateral margins are normally present in *Parolinia*.

That the stigmas are marginal in the *Cruciferae* was noticed by Robert Brown (Misc. Bot. Works, i. p. 558); so that the anomaly of their position over or opposite the placentas disappears. Fig. 17, Tab. XXV. (copied from Duchartre *l.c.*), shows these marginal placentas and stigmas developed on a carpellary stamen. The same stamen also shows (fig. 18) how the replum is formed, viz. by a prolongation of the outer side of the margins, the ovules being produced at a short distance within the edge. Lastly, fig. 19 (also from Duchartre) illustrates one of many combinations of carpellary stamens, in which the kind of arrest of the placentas and ovules I have spoken of, and which I conceive takes place along the median line of each valve, is seen at *a*. It may be observed, lastly, that the dehiscence of the siliqua, indicated at * in fig. 16, is, according to the above interpretation, strictly loculicidal, perhaps the commonest of all the methods, and is thus relieved of all the abnormal appearances.

There are some fruits of the *Cruciferae* in which the venation is conspicuous, and would seem to corroborate this view. Thus in *Lunaria* and *Iberis*, for example, the transverse and branching veins are given off from the margins of the valve, and terminate by anastomosing on the median line. In other cases, where the venation is more obscure, a translucent line may be observed down the middle of the valve, marking, as I take it, the line of cohesion.

Besides *Parolinia*, mentioned above, *Tetrapoma* has four carpels; and *Brassica* as well as *Cheiranthus* not unfrequently develop two in addition to their normal number, under cultivation.

With reference to the supposed quinary origin of the flower, it may be observed that *Capparis* † has sometimes five petals; and *Megacarpæa*, if the figure given by Le Maout and Decaisne be true, may have exactly 10 stamens.

It may be asked on what grounds do I assume the right to suppress the fifth part of each cycle. The reply is, that such symmetrical reduction from a normal and typically higher symmetry is extremely common. Thus Rue (including *Haplophyllum*), *Adoxa*, *Hypopitys*, *Potentilla*, *Tormentilla*, &c. have habitually both 5-merous and 4-merous flowers; while the petals of *Lythrum Salicaria* range from 5 to 7 in number; similarly 4-8-merous flowers are found on Jessamine, Elder, &c.

If now we attempt to account for this reduction or increase, it is only conceivable by its being done by some similar or identical arrest or development respectively in each whorl. If, for instance, we draw alternate whorls of fives, and strike out *one* part, but *any* of each whorl, it will be seen how impossible it will be to form uniformly alternating whorls of fours out of the remaining parts. If, on the other hand, each whorl be

† I allude to *Capparis*, as whatever theory he advanced for *Cruciferae* must apply to *Capparideæ* as well.

numbered quincuncially, No. 1 of each whorl being nearest that of the preceding, and on the same side of it, and then if we strike out all those, say, numbered 5, the remaining four parts in each whorl, on closing up the gaps, instantly form regularly alternating whorls of fours. Thus, then, I conceive the cruciferous flower to have arisen by a symmetrical reduction from fives to fours—first by the arrest of development of every fifth part of quincuncially arranged whorls, then by an additional arrest of a posterior and anterior stamen of the outer whorl, as well as a partial arrest of the carpels as described above.

A botanist who accepts the idea of a Crucifer being referable to a binary symmetry, is M. Victor Meschajeff*. He regards the two stamens constituting one of the taller pairs (as also of two adjacent petals) as reversions to a primitive type, and considers that the usual free condition of the stamens is a result of *dédoublement*.

I would take this opportunity of expressing my belief that this is a fundamentally erroneous view. It seems, too, to agree with Dr. Masters's expression of "inseparate" as a substitute for "cohesion." If cohesion, however, be objected to as implying a previous condition of freedom which never existed in petals normally joined, so "inseparate" would seem to imply that union was prior to freedom. There could be no reasonable objection, as far as I see, to the term "inseparate," provided no explanation of the condition is implied, but simply the fact that the parts are "not separate." Dr. Masters, however, qualifies the term by saying that the parts thus described as inseparate are *not separated*. The use of this participle at once introduces a new idea, and implies the existence of some tendency *to separate* what was before joined. Now this seems quite as objectionable as the term cohesion seems to that author ('Botany for Beginners,' p. 27) †.

But, according to the laws of evolution, integration, where it exists, is always subsequent to isolation or freedom. The rare cases of "dialysis," as of *Convolvulus* and *Campanula* with free petals, or of "solution," as of *Pyrus* and umbelliferous flowers with an inferior calyx, would be cases of reversion; while, in the *Cruciferae*, freedom of parts, except in the gynæcium, is clearly a fundamental condition, as it has no affinity with any gamopetalous order: consequently the occasional cohesion of petals or stamens in any cruciferous flower *is not a reversion but a more advanced differentiated state*, and appears to be due simply to the close approximation of the parts thus occasionally joined.

If such a flower should ever have an apocarpous pistil, *that* would be a true instance of reversion; but no case of union could possibly be such.

For the above reasons I have always looked doubtfully on "chorisis" as a principle in flowers. Doubling or an increase of number of parts is common enough, as indeed

* Bull. de la Soc. Imp. des Nat. de Moscou, 1872, no. 2, quoted in Bull. de la Soc. Bot. de France, A, 1874, p. 16.

† Dr. Masters has been good enough to give me the following comment on these remarks:—" 'Inseparate' I apply to cases where separation of parts, though 'potential,' has not *yet* occurred, and wherein, if the course of development be arrested, it may never actually occur." But it is this very 'potentiality,' or tendency to separate parts, which I can only recognize as identical with atavism or reversion. Hence I think it ought not to be considered a principle of *development*, but rather a case of *retrogression*, and therefore exceptional.

occurs frequently in the *Cruciferae* when two stamens arise from the same quadrangular or oval gland instead of a single lateral one; but this is not that one has given rise to two, but that in addition to the normal one another is present.

If, instead of regarding only the life-history of a plant *per se*, we regard it from an ancestral point of view, then "cohesion," as of the gamopetalæ, is the most correct term; for it implies that the parts *were* originally (that is, in their ancestry) free, but are *now*, in the existing descendants, coherent; whereas "inseparate" would imply that cohesion was an antecedent condition, and that there existed an ineffectual tendency to separate the parts of a whorl.

That a cruciferous flower has arisen through insect agency I have no doubt, and strongly suspect that the lateral single stamens are specially concerned in intercrossing. On the other hand, there are several of our common cruciferous plants which are self-fertilizing, such as *Capsella*, *Lepidium*, and *Senebiera*. In some of these I have often detected the pollen-tubes penetrating the stigma even in unopened buds, as in winter. These I take to be degraded conditions. In these, too, as far as can be judged from the relative heights of the stamens and stigmas, it would seem that the four taller stamens are chiefly, if not solely, concerned in self-pollination. In *Senebiera didyma* it may be observed that there are but two stamens; and they represent the taller pairs, one for each pair respectively. This reduction is a condition not infrequent in inconspicuous self-fertilizing flowers; for the number of stamens is often reduced, as mentioned above, in the flowers of several of the *Alsineæ* which do not require insect agency.

X. Note B.—ON *Adoxa moschatellina*.

It may be interesting to some to have recorded the varieties which are found in the symmetry of the terminal as compared with the lateral blossoms. Of 71 heads of blossoms examined, all of which had the apical flower composed of whorls of fours,

- 60 had all four flowers 5-merous below,
- 3 had two 4-merous and two 5-merous below,
- 2 had three 5-merous and one 6-merous below,
- 3 had three 5-merous and one 4-merous,
- 1 had four 4-merous,
- 1 had two 6-merous and two 5-merous,
- 1 had the apical flower 5-merous, with three 6-merous and one 5-merous below.

This plant is also remarkable for the order of expansion in the different parts.

The terminal flower opens first; and its parts expand *all at once*. Of the lower flowers the two upper sepals of a flower open out first; then the two upper stamens are mature, and shed their pollen; next, the anthers below them dehisce in succession downwards, during which period the lower sepals begin to expand.

XI. Note C.—ON THE ORIGIN OF THE TERNARY AND QUINARY SYMMETRY OF FLOWERS WITH INDEFINITE AND SPIRALLY ARRANGED MEMBERS.

Calycanthaceæ.—Of the two genera comprising this order, both of which have opposite leaves, *Calycanthus* illustrates an abrupt change from opposite leaves to the $\frac{8}{21}$

arrangement in the bracts or bract-like sepals of the flower, but no differentiation occurs between the bracts, sepals, and petals respectively; whereas *Chimonanthus* (see fig. p. 191, in Le M. & D.) would seem to be a more highly differentiated type, in that not only is the calyx now distinguishable from the corolla, but five anterior stamens constitute a distinct whorl by themselves, and the indefinite barren ones of *Calycanthus* are here represented by five also.

How whorls or cycles of fives arise directly out of opposite parts has been fully described in my previous paper, quoted above, p. 181; so that I need not dwell upon it now.

Magnoliaceæ, *Berberidaceæ*, *Anonaceæ*, and *Menispermaceæ* are orders characterized by a ternary arrangement in their flowers, and by the whorls being usually double.

The origin of this might at first sight be thought to be the same as of the ternary arrangement, which is almost universal in petaloid Monocotyledons—namely, to have arisen from the tristichous phyllotaxis. But the fact that the perianth consists of 6 parts ($=3+3$) in the latter, and twice or more than double that number in some of the former, is significant, and would seem to imply a different origin, which I believe to be as follows:—For any phyllotactical arrangement corresponding to the fractions of the usual series, excepting $\frac{1}{2}$ or distichous, *every projected circle contains three leaves*; and on arresting the internodes of the flowers there always follows the tendency to alternation in position with the parts of the whorls immediately above and below. Hence the “threes” of each circle arrange themselves in a decussating manner. Thus in *Berberis vulgaris* we have 3 bracts, 6 ($=3+3$) sepals, 6 ($=3+3$) petals, 6 ($=3+3$) stamens, making in all 21 parts, corresponding to a cycle of the series $\frac{8}{21}$.

On the other hand, a flower of *Aconitum*, according to Braun, as quoted in Sachs’s Text-Book, p. 530, is composed as follows: the sepals are pentastichous, or $\frac{2}{5}$; the corolla octastichous, or $\frac{3}{8}$; the stamens $\frac{8}{21}$, and the carpels 3.

Hence it would seem that there can be at least four methods of disposing the floral members when numerous and spirally arranged, viz. :—

1. Spirally and with no breaks, then mostly $\frac{8}{21}$, e. g. *Magnolia*.
2. Broken up into fives, or $\frac{2}{5}$ arrangement . . . „ *Chimonanthus*.
3. Broken up into threes, decussating . . . „ *Berberis*.
4. Broken up into whorls of 5, 8, 21, and 3 . . . „ *Aconitum*.

XII. Note D.—ON THE NATURE OF THE COROLLA OF *Primula*.

With regard to the theory of Pfeffer (see Sachs’s Text-Book, p. 531), that in the *Primulaceæ* the corolla is an outgrowth of the androecium, I think there is more than one argument against it. Not only would the whole of the *Myrsineæ* have to be interpreted in a similar manner, but all analogy seems opposed to it. That the stamens are opposite the petals is true; but then *Samolus*, with its staminodia alternating with the petals, throws light upon this peculiarity; and if we examine the fibro-vascular bundles, it will be seen that ten pass into the tube of the corolla, five larger ones up the middle of each lobe, and *five smaller ones are intermediate*; each of the larger sends off a *small* bundle to the stamen adherent to the petal, respectively. The main portion

of the bundle continues its way to the notch at the summit of the lobe, and branches within the lobe. Now this is identically the same as in the calyx of *Prunus*, in which, as in the corolla of *Primula*, there are five median bundles, which do not bifurcate until they arrive at the lobes. The five bundles alternating with the petal-lobes of *Primula* or calycine lobes of *Prunus* bifurcate also on arriving at the notch between the lobes. They then send off dichotomously branching members up the adjacent edges of two lobes—that is, of two different members of the whorl.

The conclusion I would draw is this—that the calyx-tube of *Prunus* is homologous with the petioles, the lobes with the blades, and that the same holds good for the corolla of *Primula*; and I think we are justified in concluding that the corolla of the latter is a veritable foliaceous whorl.

Moreover the æstivation of the corolla of Primrose is strictly the same as in many other plants, and, if analogy is to be trusted, confirms this belief. Lastly, what is of chief importance is, that the theory being based, as no doubt is the only sound method, on development, is, however, as I interpret the facts, based on a misunderstanding of them—namely, that *because* the stamens appear first, and the lobes of the corolla *subsequently* (but they arise as soon as the anther is developed, *and are all connected by a horizontal band*), *therefore* the latter is an outgrowth of the andrœcium. But, as has been already observed, invariably acropetal or centripetal development of the whorls of flowers does not occur. That the corolla-lobes should develop *after* the stamens is by no means without parallel; for it occurs in many plants, as in the few following examples, in which the whorls are written in order of development:—

Ranunculus acris: Cal., St., Pi., Cor.

Stellaria holostea: Cal., St. opp. pet., St. opp. sep., Pi., Cor.

Lychnis dioica: same order, but without Pi.

Veronica chamædrys: Cal., St., Pi., Cor.

Cerastium glomeratum (self-fertilizing): Cal., Pi., St. opp. sep., St. opp. pet., Cor.

Arenaria trinervis (do.): same order.

