II. "On Leaf-Arrangement." By HUBERT AIRY, M.A., M.D. Communicated by CHARLES DARWIN, F.R.S. Received March 23, 1874.

(Abstract.)

This paper is offered in correction and extension of the views contained in a previous paper by the same author, read 27th February, 1873.

The main facts of leaf-arrangement to be accounted for are :—

(1) the division into *verticillate* and *alternate* leaf-order;

(2) in the former, the equal division of the circumference of the stem by the leaves of each whorl, and the alternation, in angular position, of successive whorls;

(3) in the latter, the arrangement of leaves in a spiral series round the stem, with uniform angular divergence between successive leaves, and the limitation of that angular divergence (represented as a fraction of the circumference) to certain fractional values (in most cases only approximate) which find place most commonly in the following convergent series (A) :—

$$\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \frac{13}{34}, \frac{21}{55}, \frac{34}{89}, \frac{55}{144}, \text{\&c.}; \ldots\ldots\ldots\ldots (A)$$

more rarely in the following (B):—

$$\frac{1}{3}, \frac{1}{4}, \frac{2}{7}, \frac{3}{11}, \frac{5}{18}, \frac{8}{29}, \frac{13}{47}, \text{\&c.}; \quad \ldots\ldots\ldots\ldots\ldots\ldots \text{(B)}$$

very rarely in the following (C):—

$$\frac{1}{4}, \frac{1}{5}, \frac{2}{9}, \frac{3}{14}, \frac{5}{23}, \text{\&c.}; \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{(C)}$$

besides a few isolated values, $\frac{2}{11}$, $\frac{2}{13}$, $\frac{1}{8}$, &c., which would find place in higher series. (Hofmeister, 'Allgemeine Morphologie der Gewächse,' p. 449. Leipzig, 1868.)

Dealing first with the phenomena of *alternate* leaf-order, the theory is advanced that, in each of the series A, B, C, &c., the higher orders have been derived from some lower order of the same series by a process of condensation advantageous to the species in which those higher orders are found; that the scene of this condensation of leaf-order has been the bud and other close-packed forms of plant-growth; and that the immediate gain has been better economy of space.

In support of this theory it is argued, first, that the *use* of leaf-order is to be found in that stage of the life of a shoot in which the leaf-order is most regular and perfect. Leaf-order is seen in perfection in close-packed forms of plant-growth, such as the *bud*, the *bulb*, the *radical rosette*, the *involucre*, the *composite head*, the *catkin*, the *cone*, even the *seed* itself. Therefore it must be in these forms that leaf-order is especially useful. In elongated shoots, on the contrary, with long internodes and distant leaves, the leaf-order has a tendency to lose that regularity which it enjoyed in the bud, and is often disarranged by a twist of the stem or by contortion of the leaf-stalks (required for the better display of the leaf-blades to the light). The native arrangement of the leaves (excluding the order $\frac{1}{2}$) is often a positive disadvantage to them in lateral twigs. It is only in the more vertical and unembarrassed shoots that the leaf-blades remain content with their distributive position. Indeed, one chief use of the leaf-stalk seems to be to enable the leaf-blade to make the best of an unfavourable birth-place. (Yew, silver fir, box, and privet are instanced as examples.) Hence it appears probable that the use of leaf-order is not to be found in the elongated shoot.

Looking, then, to the above-mentioned close-packed forms of plant-growth as the scene of the usefulness of leaf-order, it is seen that the characteristic feature which distinguishes them from the elongated forms is *contact* between neighbouring leaves (or shoots). The whole surface of the stem is occupied by their bases, and no vacant interstices are left between them. It is plain that the process of cell-growth has resulted in great *mutual pressure* between neighbouring leaves and shoots. Recognizing this fact of mutual pressure, we can see that leaf-order is useful in these close-packed forms by securing equal development of leaves and therefore economy of space. If the whole space is to be occupied, and the leaves or shoots are to have equal development, there must be orderly arrangement of some kind. The principle of economy of space under mutual pressure is put forward as of chief importance in leaf-arrangement.

It appears that economy of space is especially demanded in a longitudinal direction, for the sake of protection against vicissitudes of temperature and the attacks of enemies. In a bud, for example, it is evidently important, on the one hand, that as many leaves as possible should attain as high development as their situation will allow, in order that they may be ready at the first approach of spring to complete that development and enter on their function without loss of time; but, on the other hand, it is evidently important that the embryo shoot should be as short as possible, in order that it may be well within the guard of the protecting scales and less exposed to danger during the long period of bud-life. These claims will be satisfied by a vertical condensation of the leaf-order, such as the state of mutual pressure of the embryo leaves and shoots is calculated to bring about.

That the arrangements represented by the lower terms of the abovementioned series A, B, C, &c. would, under a force of longitudinal condensation, actually give rise to the successive arrangements represented by the higher terms of the same series, is shown by diagrams, in which the necessary consequences of each step of condensation are made apparent to the eye. In these diagrams a leaf or shoot is represented (for mechanical considerations) by a sphere, and the spheres are numbered from 0 upwards. Taking, first, series A, the lowest order of that series, $\frac{1}{2}$, is represented by two vertical rows of spheres, those of each row being in contact and alternating with those of the other. If these two rows remain vertical, no longitudinal condensation can take place. The first step towards such condensation must be their spontaneous deviation from the vertical. (Instances of such deviation in nature are found in the genus *Gasteria* and others, to be considered further on.) The next step required is some force of vertical compression, such as would result in nature from the stunting of the bud-axis (due directly to cold or indirectly to the advantage of protection gained thereby), attended with less, if any, stunting of the leaves. Then it is seen that the successive stages of condensation, beginning with the order $\frac{1}{2}$, will bring successively into contact with 0 (zero) the following numbers, 3, 5, 8, 13, 21, 34, 55, 89, 144, &c., alternately to right and left, producing in succession a series of orders which exactly resemble those found in nature, represented approximately by the successive terms of series A:—

$$\frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \frac{13}{34}, \text{ \&c.}$$

The first two or three stages of this process may be illustrated by mechanical experiment. Attach two rows of light spheres in alternate order on opposite sides of a stretched india-rubber band, give the band a slight twist, and relax tension; the system rolls up with strong twist into a tight complex order with three steep spirals, an approximation to the order $\frac{1}{3}$: if the spheres are set a little away from the axis, the order becomes condensed into (nearly) $\frac{2}{5}$, with five nearly vertical ranks; and it is plainly seen that further contraction, with increased distance of the spheres from the axis, will necessarily produce in succession the orders (nearly) $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, &c., and that these successive orders represent successive maxima of stability in the process of change from the simple to the complex. These results are not invalidated by the consideration that the natural development of leaves is not simultaneous but successive.

By other diagrams it is shown that the same process of condensation operating on the orders represented by the lower fractions of series B $\left(\frac{1}{3}, \frac{1}{4}, \text{ \&c.}\right)$ will produce the higher orders of that series.

The same is also shown for series C $\left(\frac{1}{4}, \frac{1}{5}, \text{ \&c.}\right)$.

From the striking correspondence thus brought out between fact and theory, the conclusion is anticipated that we have here a clue to the secret of complex spiral leaf-order—that it is the result of condensation operating on some earlier and simpler order or orders, the successive stages of that condensation being ruled by the geometrical necessities of mutual accommodation among the leaves and axillary shoots under mutual pressure in the bud (taking the bud as the type of close-packed forms).

From this point of view, Hofmeister's law, that every leaf is found at that point in the circumference of the stem which has been left most open by the earlier leaves of the cycle, means that every leaf stands in that position relative to its neighbours which gave it most room for development in the bud.

Allusion was made above to deviation of leaf-ranks from the vertical as a necessary first step towards condensation. A series of six diagrams shows the gradual transition presented by different species of the South-African genus *Gasteria*, from a form in which the two ranks are exactly vertical, to a form in which they are strongly twisted into a complex order with angular divergence nearly $\frac{3}{7}$, differing from $\frac{2}{5}$ by only $\frac{1}{35}$ of the circumference, and evidently admitting of further twist and closer approximation to the order $\frac{2}{5}$. From this striking series it is inferred that ranks originally vertical can and do acquire and transmit a tendency to deviate from the vertical, and that this tendency admits of augmentation to a high degree.

Assuming a twist, then, as a probable primary variation from an originally vertical condition of leaf-ranks, it is plain that each leaf would take a lower position, and the whole bud (with the same number of leaves) would be shorter, than in the untwisted form. The shorter bud, it is supposed, would have an advantage in cold seasons. The direct action of cold, by stunting the bud-axis (provided it did not stunt the leaves in the same proportion), would increase the twist. It may fairly be supposed that this twist would be taken advantage of and increased by natural selection in subservience to the close packing of the leaves. This course of modification is equivalent to the continued action of a force of vertical compression (mentioned above as the second requisite for condensation).

Transition similar to that in *Gasteria* is seen in the genus *Aloë*. Compare the two vertical ranks of *A. verrucosa* with the two twisted ranks of *A. obliqua*. In *A. serra* (Sachs, 'Lehrbuch der Botanik,' fig. 144) the change from the vertical to the strongly twisted form is found in the same plant: the basal leaves are in order $\frac{1}{2}$; the higher take complex order.

Exactly comparable (in this respect) with *Aloë serra* are the common laurel, Portugal laurel, Spanish chestnut, ivy, and others, which exhibit a similar change of leaf-order. These instances agree in presenting the complex order in the buds or parts of buds which occupy the most exposed situations, while they retain the simple order $\frac{1}{2}$ in the less exposed lateral buds or in their basal portion. The exposure in the former case may be regarded as a sample of that which, in the course of many generations, has (it is supposed) occasioned the condensation of leaf-order.

It is here contended that the force of gravity (to which the two-ranked leaf-order of lateral twigs is referred by some authors) could not have been equally the cause of the phenomena seen in the inclined lateral shoot of Spanish chestnut and in the upright *Aloë serra*: but the phenomena in the two cases are the same, and admit of a common explanation by the condensation theory, if we regard the basal portion of the shoot as retaining the ancient order, and the more exposed terminal portion as having undergone protective modification.

The various degrees of obliquity of spiral ranks in the alternate orders of leaf-arrangement, and the complicated numerical relations existing between those various ranks, are all fully accounted for by the condensation theory.

Analyzing the spiral arrangement seen in a sunflower-head, a dandelion-head, a house-leek rosette, and an apple-twig, the result is found to be that any leaf (or fruit, in the first two instances), taken as zero, has for next neighbours successively, in rising steps of complexity of order, the 1st, 2nd, 3rd, 5th, 8th, 13th, 21st, 34th, 55th, 89th, 144th, &c. (in order of growth) alternately on the right side and on the left, producing alternately right- and left-handed spirals in sets of 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, &c.; and these numbers are identical with those which would result from condensation of one of the lower orders of series A. Similar considerations apply to series B and C.

It is a significant relation that, in the sunflower and similar examples, the arrangement of the fruits in the composite head is such as would result from condensation of the arrangement of the leaves on the stem.

Among the *whorled* orders also there is equally strong evidence of the working of the same force of condensation.

First there is a series (α) derivable from the crucial arrangement. (This is shown by diagrams.) In the orders thus formed it is seen that conspicuous sets of parallel spirals will form the most striking feature, and that these spirals will be found in sets of 2, 4, 6, 10, 16, 26, 42, &c. (series α).

Instances are seen in the genera *Mercurialis* and *Sagina*, and the order *Dipsaceæ*, in which last the whole series α finds exemplification.

Here also it is a significant relation that the fruit-order in the composite heads of *Dipsaceæ* is such as would result from condensation of the crucial order of their stem-leaves. Some of these plants exhibit in their radical leaves a minor degree of the same condensation.

In like manner it is shown that condensation of whorls of three would produce orders with spirals in sets of 3, 6, 9, 15, 24, 39, 63, &c. (series β). For examples see Hofmeister, *op. cit.* p. 460.

Condensation (if any) of whorls of four would give spirals in sets of 4, 8, 12, 20, 32, &c. (series γ).

It is contended that the preceding evidence, drawn from both divisions of leaf-arrangement (alternate and whorled), is sufficient to establish the principle of condensation as having played an important part in the history of leaf-arrangement.

But there are phenomena in leaf-arrangement which are *not* explained by condensation. We have still to account for (1) the origin of alternate orders with 3, 4, 5, 7, 9, &c. vertical ranks; and (2) the origin of the different whorled orders, with whorls of two, three, four, five, &c. (with 4, 6, 8, 10, &c. vertical ranks).

The whole course of condensation depended on obliquity of ranks; but the distinguishing feature in these cases is that the ranks are exactly or almost exactly vertical.

All these cases are explained on the hypothesis that there has been in the vegetable kingdom a variability (*per saltum*) in the number of leaf-ranks; that a plant originally having two vertical ranks has, by a stroke of variation, produced shoots or seedlings with three vertical ranks; that three have varied to four, four to five, five to six, and so on; and that these "sports" have survived in some cases because of some advantage which they enjoyed (probably the same advantage as that gained by condensation—the accommodation of the same number of leaves in a shorter bud).

This hypothesis is supported by the variability which is found at the present day in the number of leaf-ranks in one and the same species. For instance, *Sedum sexangulare* exhibits *seven* nearly vertical ranks in order $\frac{2}{7}$, or *six* exactly vertical in whorls of three. *Fraxinus excelsa* has normally *four* exactly vertical ranks in whorls of two, but may be found with *five* nearly vertical ranks in order $\frac{2}{5}$, or with *six* exactly vertical in whorls of three. (These three varieties may be found on shoots growing from the same stump.) Whorls of three are often produced by plants usually bearing whorls of two (*e. g.* sycamore, lilac, laurustinus, maple, horse-chestnut, elder, ash, &c.), and whorls of four instead of three are seen in some species of *Sedum* and *Verbena.* Among these forms it does not seem possible that one could be produced from another by accumulative modification.

Professor Beal has found well-marked variation in the cones of larch, spruce, &c., the majority belonging to series A, but a considerable minority to series B or series α.

In dandelion-heads about 5 per cent. belong to series α.

Different species of the same genus (e. g. *Aloë verrucosa* and *variegata*, *Haworthia viscosa* and *pentagona*, and different species of *Sedum* and *Cactus*) often exhibit differences of leaf-order which can hardly be understood but as resulting from direct variation in number of leaf-ranks.

This hypothesis is also supported by analogy drawn from the animal kingdom. Among starfishes there is variability in the number of rays: *Asterias rubens* has sometimes four or six instead of five; *A. papposa* has from twelve to fifteen. Among mammals there is some variability in the number of digits.

Supposing, then, that, by strokes of variation, forms have been produced with (2) 3, 4, 5, 6, &c. vertical leaf-ranks, it is next to be considered how the arrangement of the leaves in each form would be affected by the demands of economy of space and mutual accommodation of ranks, supposing the ranks to be similar in point of size and number of leaves.

Two vertical ranks would gain lateral accommodation by taking alternate order $\frac{1}{2}$. Under vertical condensation, with twist in either direction, they would give rise to the successive orders of series A. (Two ranks are found in uneconomical opposite order in the genus *Mesembryanthemum.* This arrangement would be prone to fall into crucial order under vertical compression.)

Three vertical ranks would, with least surrender of lateral accommodation, assume alternate order $\frac{1}{3}$ (illustrated by diagram). A slight twist in one direction (No. 3 towards No. 1) would allow perfect lateral accommodation. In three-ranked plants (e. g. *Carex* and *Alnus*) such twist is usually found. Vertical condensation operating on three ranks possessing this obliquity would produce subsequent orders of series A. If the obliquity were in the opposite direction (No. 3 towards No. 2), condensation would produce successive orders of series B.

Four vertical ranks would economically fall into crucial order, the members of each rank fitting into the intervals between those of its neighbours. Opposite members therefore would stand at the same height, and would occupy one and the same node; they would also divide the circumference equally, and would stand over the intervals of the next lower pair. This crucial order under vertical condensation would produce series *α*. In rare cases four ranks might assume an alternate order $\frac{1}{4}$. Vertical condensation of this order $\frac{1}{4}$ with twist (No. 4 towards No. 1) would produce series B; with opposite twist (No. 4 towards No. 3) it would produce series C.

Five vertical ranks would, with least surrender of lateral accommodation, assume alternate order $\frac{2}{5}$. A slight obliquity (No. 5 towards No. 2), such as is usually found in nature, would allow perfect lateral accommodation. Condensation would then produce further orders of series A. With opposite obliquify (No. 5 towards No. 3) a new series $\left(\frac{2}{5}, \frac{3}{7}, \frac{5}{12}, \frac{8}{19}, \text{\&c.}\right)$ would be produced. Five ranks might also take alternate order $\frac{1}{5}$, which, condensed, would give with one twist series C, with the other a new series $\frac{1}{5}, \frac{1}{6}, \frac{2}{11}, \frac{3}{17}$, &c.

Six vertical ranks would economically fall into whorls of three, the members of each whorl dividing the circumference equally, and standing over the intervals of the next lower whorl. Condensation would give series β. If six ranks should fall into alternate order $\frac{1}{6}$, one obliquity would lead to a series $\frac{1}{6}, \frac{1}{7}, \frac{2}{13}, \frac{3}{20}$, &c., the opposite to a series $\frac{1}{6}, \frac{2}{11}, \frac{3}{17}$, &c.

Seven vertical ranks would take alternate order $\frac{2}{7}$, facilitated by obliquity. Condensation would give series B. (It is needless to follow other possible lines of condensation.)

Eight vertical ranks would fall into whorls of four, with the same general characters noted above in whorls of two and three. Condensation would give series γ.

Nine would give $\frac{2}{9}$. Condensation would produce series C.

Ten would give whorls of five.

Eleven would give $\frac{2}{11}$.

Twelve would give whorls of six.

Thirteen would give $\frac{2}{13}$; and so on.

Thus it appears that the *whorled* orders would naturally arise from economic arrangement of *even* numbers (except 2), and the *alternate* orders from economic arrangement of *odd* numbers (including also 2), of vertical ranks.

It also appears that, in the whorled division, the members of each whorl will divide the circumference of the stem equally, and that successive whorls will alternate in angular position.

It has already been shown that in the alternate division the spiral arrangement of the leaves, with angular divergence limited to certain series of fractional values (A, B, C, &c.), would follow on the hypothesis of condensation.

These are the "main facts of leaf-arrangement" set down on page 298 to be accounted for.

It is possible that all the varieties of leaf-order at present existing may have been derived from an original two-ranked arrangement, partly by variation in the number of leaf-ranks, and partly by vertical condensation of the orders so formed. This view is supported by

(1) the high probability that the simplest form has been the earliest;
(2) the prevalence of the two-ranked form among lower phanerogamous plants (e. g. *Gramineæ*);
(3) the numerous instances of transition from a two-ranked order at the base of a shoot to a more complex order in the higher parts;
(4) the prevalence of the two-ranked arrangement of rootlets on

roots, taken in connexion with their probable homology with lateral shoots (the three ranks of rootlets in *Polygonaceæ*, and the four in carrot and parsnep, illustrate variability in number of ranks);

(5) the two-ranked arrangement of leaves in the seeds of Monocotyledonous plants, as compared with the more condensed (though probably at first two-ranked) order in the more highly developed Dicotyledonous embryo.

Summary.—The author is led to suppose :—

I. That the original form of leaf-arrangement was two-ranked.

II. That this original two-ranked form gave rise to forms with 2, 3, 4, 5, 6, 7, &c. ranks, by "sporting," as opposed to any process of accumulative modification.

III. That of the orders so formed those with an even number of ranks (except 2) have, as a rule, assumed a *whorled* arrangement, and those with two or an odd number of ranks have assumed an *alternate* arrangement, under the need of lateral accommodation of ranks in the bud (taken as type of close-packed forms).

IV. That all these orders have been subject to vertical condensation, under the need of vertical economy of space in the bud (taken as type of close-packed forms).

V. (*a*) That such condensation, operating on a 2-ranked, or 3-ranked, or 5-ranked alternate order $\left(\frac{1}{2}, \frac{1}{3}, \frac{2}{5}\right)$, has produced subsequent orders of series A $\left(\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \frac{13}{34}, \frac{21}{55}, \frac{34}{89}, \frac{55}{144}, \&c.\right)$.

(*b*) That condensation of a 7-ranked $\left(\frac{2}{7}\right)$ or rarely of a 3- or 4-ranked $\left(\frac{1}{3}, \frac{1}{4}\right)$ alternate order has produced subsequent orders of series B $\left(\frac{1}{3}, \frac{1}{4}, \frac{2}{7}, \frac{3}{11}, \frac{5}{18}, \&c.\right)$.

(*c*) That condensation of a 9-ranked $\left(\frac{2}{9}\right)$ or rarely of a 4- or 5-ranked $\left(\frac{1}{4}, \frac{1}{5}\right)$ alternate order has produced subsequent orders of series C $\left(\frac{1}{4}, \frac{1}{5}, \frac{2}{9}, \frac{3}{14}, \frac{5}{23}, \&c.\right)$.

(*d*) That condensation of a 4-ranked whorled order (whorls of two) has produced successive orders of series α, with spirals in sets of 4, 6, 10, 16, 26, 42, &c.

(*e*) That condensation of a 6-ranked whorled order (whorls of three) has produced successive orders of series β, with spirals in sets of 6, 9, 15, 24, 39, &c.

(*f*) That condensation (if any) of an 8-ranked whorled order (whorls of four) would produce successive orders of series γ, with spirals in sets of 8, 12, 20, 32, &c. Higher numbers of ranks would lead to higher series.