M. Pisani has ascertained that the variety from Montebras yields:—

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|---|---|
| Fluorine | 2·27 |
| Phosphoric acid | 34·30 |
| Alumina | 38·25 |
| Water | 26·60 |
| | 101·42 |
| Specific gravity | 2·33 |

*February* 27, 1873.

WILLIAM SPOTTISWOODE, M.A., Treasurer and Vice-President, in the Chair.

The following communication was read:—

"On Leaf-Arrangement." By HUBERT AIRY, M.A., M.D. Communicated by CHARLES DARWIN, F.R.S. Received January 21, 1873.

(Abstract.)

Assuming, as generally known, the main facts of leaf-arrangement,—the division into the whorled and spiral types, and in the latter more especially the establishment of the convergent series of fractions, $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, $\frac{13}{34}$, $\frac{21}{55}$, $\frac{34}{89}$, $\frac{55}{144}$, &c., as representatives of a corresponding series of spiral leaf-orders among plants,—we have to ask, what is the meaning that lies hidden in this law?

Mr. Darwin has taught us to regard the different species of plants as descended from some common ancestor; and therefore we must suppose that the different leaf-orders now existing have been derived by different degrees of modification from some common ancestral leaf-order.

One spiral order may be made to pass into another by a twist of the axis that carries the leaves. This fact indicates the way in which all the spiral orders may have been derived from one original order, namely by means of different degrees of twist in the axis.

We naturally look to the simplest of existing leaf-orders, the two-ranked alternate order $\frac{1}{2}$, as standing nearest to the original; for it is manifest that the orders at the other extreme of the series (the condensed arrangement of scales on fir-cones, of florets in heads of *Compositæ*, of leaves in close-lying plantains, &c.) are special and highly developed instances, to meet special needs of protection and congregation: they are, without doubt, the latest feat of phyllotactic development; and we may be sure that the course of change has been from the simple to the complex, not the reverse. This point will be illustrated by experiment below.

But first, what are the uses of these orders? and at what period of the leaf's life does the advantage of leaf-order operate? The period must be that at which the leaf-order is most perfect: not, therefore, when the twig is mature, with long internodes between the leaves, but while the twig and its leaves are yet *in the bud*; for it is in the bud (and similar crowded forms) that the leaf-order is in perfection, undisturbed by contortions or inequalities of growth; but, as the bud developes into the twig, the leaves become separated, the stem often gets a twist, the leaf-stalks are curved and wrung to present the blades favourably to the light, and thus the leaf-order that was perfect in the bud is disguised in the grown twig.

In lateral shoots of *yew* and *box* and *silver fir* we see how leaves will get their stalks twisted to obtain more favourable exposure to light; and if general distribution round the stem were useful to the adult leaves, we should expect the leaves of a vertical *elm*-shoot (for example) to secure such distribution by various twists of stalk and stem; but the leaf-blades of the elm keep their two ranks with very great regularity. This goes to show that it is not in the mature twig that the leaf-order is specially advantageous.

In the *bud* we see at once what must be the use of leaf-order. It is for *economy of space*, whereby the bud is enabled to retire into itself and present the least surface to outward danger and vicissitudes of temperature. The fact that the order $\frac{1}{2}$ does not exhibit this advantage in any marked degree, supports the idea that this order is the original from which all the more complex spiral orders have been derived.

The long duration of the bud-life as compared with the open-air life of the leaf gives importance to the conditions of the former. The open-air life of the bud is twelve months, and adding the embryo life of the bud, we have about a year and a half for the whole life of the bud; and for the twelve months of its open-air life it is in a state of siege, against which a compact arrangement of its embryo-leaves within must be of great value. But the open-air life of the unfolded leaves is (except in evergreens) not more than six months.

That the order $\frac{1}{2}$ would under different degrees of contraction (with twist) assume successively the various spiral orders that exist in nature, in the order of their complexity, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, &c., may be shown by the following experiment:—

Take a number of spheres (say oak-galls) to represent embryo leaves, and attach them in two rows in alternate order ($\frac{1}{2}$) along opposite sides of a stretched india-rubber band. Give the band a slight twist, to determine the direction of twist in the subsequent contraction, and then relax tension. The two rows of spheres will roll up with a strong twist into a tight complex order, which, if the spheres are attached in close contact with the axis, will be nearly the order $\frac{1}{3}$, with three steep spirals. If the

spheres are set a little away from the axis, the order becomes condensed into (nearly) $\frac{2}{5}$, with great precision and stability. And it appears that further contraction, with increased distance of the spheres from the axis, will necessarily produce the orders (nearly) $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, &c. in succession, and that these successive orders represent successive *maxima* of stability in the process of change from the simple to the complex.

It also appears that the necessary sequence of these successive steps of condensation, thus determined by the geometry of the case, does necessarily exclude the non-existent orders, $\frac{1}{4}$, $\frac{2}{7}$, $\frac{3}{7}$, $\frac{4}{9}$, $\frac{4}{11}$, &c.

Numbering the spheres from 0 upwards, it appears that, under contraction, the following numbers are brought successively into contact with 0, alternately to right and left:—1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, &c. None of them stands vertically above 0 while in contact with it, but a little to the right or a little to the left; and so far the results of this experiment fall short of the perfect fractions $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{15}$ &c.: but in this very failure the results of the experiment are more closely in agreement with nature than are those perfect fractions themselves; for those fractions give the angular divergence only in round numbers (so to speak), and lose account of the little more, or the little less, which makes all the difference between a vertical rank and a spiral. In the large majority of spiral-leaved plants, one has to be content with "$\frac{2}{5}$ nearly" or "$\frac{3}{8}$ nearly," and it is difficult to find a specimen in which the fraction represents the order exactly.

The geometrical relations of the members of the above series 1, 2, 3, 5, 8, 13, &c. are as simple as their numerical relations.

Analysis of the order seen in the head of the sunflower and other examples, by consideration of their several sets of spirals, presents a striking agreement with the above synthetical process. In the sunflower, a marginal seed taken as 0 is found to be in contact with the 34th, the 55th, and the 89th (counted in order of growth), and even with the 144th, if there is not contact with the 34th. The dandelion, with a lower degree of condensation, has 0 in contact with the 13th, the 21st, and the 34th in large specimens; the house-leek in its leaf-order has 0 in contact with the 5th, 8th, and 13th; the apple-bud has 0 in contact with the 2nd, 3rd, and 5th; and thus we see that in nature the very same series of numbers is found to have contact-relation with 0, which we have already seen possessing that relation in the experimental condensation of the order $\frac{1}{2}$.

Difference of leaf-order in closely allied species (e.g. *Plantago major* and *P. coronopus*) is found in close relation to their different habits and needs.

The prevalence of the order $\frac{1}{2}$ in marine *Algæ*, and in *Gramineæ*, a low-developed gregarious group, and its singular freedom from individual

variation in that group and in elm, beech, &c., support the view that this order is the original of the spiral orders.

In many plants we find actual transition from the order $\frac{1}{2}$ to an order more complex, as, for instance, in *Spanish chestnut*, *laurels*, *nut*, *ivy*; and these instances agree in presenting the complex order in the buds that occupy the most exposed situations, while they retain the simple $\frac{1}{2}$ in the less exposed lateral buds. Several kinds of *aloe* have the order $\frac{1}{2}$ in their basal leaves and a higher order in the remainder. A species of *cactus* often contains a complete epitome of phyllotaxy in a single plant or even in a single shoot.

Shoots of *acacia* often present a zigzag disposition of their leaves, on either side of the branch, which seems unintelligible except as a distortion of an original two-ranked order.

The prevalent two-ranked arrangement of rootlets or roots seems to be a survival underground of an order which originally prevailed through the whole plant, root, stem, and branch.

In the whole Monocotyledonous class the first leaves in the seed have the order $\frac{1}{2}$.

In the Dicotyledonous class the first leaves in the seed have the simplest order of the whorled type.

As the spiral orders have probably been derived from a two-ranked alternate arrangement, so the whorled orders have probably been derived from a two-ranked *collateral* (two abreast) arrangement. This is illustrated by an experiment similar to the former; and it is seen that successive parallel horizontal pairs of spheres are compelled under contraction to take position at right angles to one another, exactly in the well-known crucial or decussate order. These whorls of two contain potentially whorls of three and four, as is seen in variations of the same plant; but the experiment does not show the change.

The reason of the non-survival of the (supposed) two-ranked *collateral* order lies in its manifest instability; for under lateral pressure it would assume the alternate, and under vertical the crucial order.

The bud presents in its shape a state of equilibrium between a force of contraction, a force of constriction, and a force of growth.

To sum up, we are led to suppose that the original of all existing leaf-orders was a two-ranked arrangement, somewhat irregular, admitting of two regular modifications, the alternate and the collateral; and that the alternate has given rise to all the spiral orders, and the collateral to all the whorled orders, by means of advantageous condensation in the course of ages.