INTRODUCTION.

The subject of the present paper is one which generally proves void of much attraction, except to those botanists who are interested in mathematical calculations. It may, therefore, be advisable to preface a few words in explanation of its appearing in the Transactions of the Victoria Institute.

The Rev. Walter Mitchell's interesting lecture on the Bee-cell, delivered at the Anniversary Meeting of 1870, drew from the writer a few remarks tending to show that the fact of organic forces acting under some impulse, and producing exact results, though rare under any circumstances, was not confined to the animal kingdom, but occurs also in the arrangement of leaves.

It was in consequence of these remarks that I was requested to bring before this Society some more detailed account of the principles of this remarkable phenomenon, or, as it has been called, Phyllotaxis, and so furnish the members of the Victoria Institute with a paper as companion to, though by no means so equally attractive as that of Mr. Mitchell on the bee-cell. That an insect should possess the power of practically, yet unconsciously working out for its own purposes a high mathematical problem is probably the most mysterious of Nature's gifts to her creatures. The bee knows nothing of geometry, and we can only say that it acts instinctively under direction. The cell is one of the rare examples of the issue of organic forces being rigidly demonstrable by aid of the exact sciences.

In the mineral kingdom, on the other hand, it is the rule, rather than the exception, to find the issue of natural forces, either singly or in their resultant, to be capable of mathematical expression; e.g., the crystallographic forms of minerals.

But when we turn to the vegetable kingdom, we are again amongst organic forces, and we look about almost in vain for results which can be tested by mathematics or which can be represented by their formulae. The most remarkable instance is probably the arrangement of leaves, and which forms the subject of the present paper.
1. If several leafy shoots from different plants be taken, it will be observed that many, probably the majority, have their leaves placed one at a time on the stem; or, as botanists say, *alternately*; e.g., the Garden Flag, a Sedge, the Oak, and the Holly. The rest will almost always have two leaves at the same position (or node), but situated on opposite sides of the stem; e.g., Lilac, Privet, or Horse-chestnut. Of the latter, it will be also noticed that each pair of leaves stands at right angles to those above and below it. Such series of pairs of opposite leaves constitute what has been called the *decussate* arrangement. Extended observations will only strengthen the conclusion that leaves are for the most part *alternate* or *opposite.*

2. **Alternate Leaves.**—If I take a branch of the May or Oak, and hold it vertically with any selected leaf before me, and then pass my finger upwards along the stem from that leaf to the next, and thence to the third, fourth, fifth, and sixth leaf in succession, I find that the one last reached (sixth) is exactly over, or in the same vertical line with, the first; and if I proceed further, I shall find the seventh is vertically over the second, the eighth over the third, and so on, the eleventh being, therefore, over both the sixth and first.

3. The following observations will result from this examination:—Obs. 1. All the leaves on the branch are arranged in five vertical rows: from this fact such an arrangement has been called *pentastichous.* Obs. 2. The imaginary line traced by the finger in passing from leaf to leaf successively is a spiral line. Obs. 3. This spiral line *coils twice* round the stem before arriving at the sixth leaf; the portion of the spiral intercepted between the first and sixth leaf is called a *cycle.* Obs. 4. A cycle contains *five leaves,* the sixth being the first leaf of the succeeding cycle.

4. The method adopted to represent this arrangement is by means of the fraction \(\frac{2}{5}\). The numerator (2) indicates the *number of coils in a cycle.* The denominator (5) shows the *number of leaves in a cycle.*

5. Let a complete cycle be projected on a plane surface, and represented by a “helix” (a spiral line like a watch-spring) having two complete coils, and let the corresponding positions of the leaves be marked upon it. Then if radii be drawn from the centre to the positions of the leaves, the angle between those drawn to any two successive leaves will be two-fifths of a whole circumference, or of 360°; *i.e.* it will contain 144 degrees. From this fact, the fraction \(\frac{2}{5}\) is called the *angular divergence* of the pentastichous arrangement of leaves. An observation of

*Leaves will occasionally be found grouped in threes or some higher number; they are then said to be *whorled* or *verticillate.*
some importance may be here conveniently made; viz., that each coil (i.e. the circumference of a circle) contains three leaves; this same number is invariably true for all other arrangements of the “primary” series, as will be hereafter described.

6. Let another example be taken. Suppose it to be a sedge (Carex). Here the fourth, seventh, tenth, &c., leaves will all be found arranged vertically over the first; the fifth, eighth, eleventh, &c., over the second; and the sixth, ninth, twelfth, &c., over the third. Hence there will be only three vertical rows of leaves, and the name given to this arrangement is consequently tristichous. Moreover, it will be observed that there are but three leaves in each cycle, and that the cycle completes but one coil or circle in passing from any leaf to the next immediately over it; so that by adopting the method given above, of representing this arrangement, by a fraction, the fraction will be \( \frac{1}{3} \), and the angular divergence will be \( \frac{1}{3} \) of 360°, or 120 degrees.

7. By extending such observations as these, we should soon discover other arrangements of leaves to exist in nature; and we should find that their angular divergences are equally capable of being represented by fractions. Thus, in the Garden Flag (Iris), the leaves are on opposite sides of the stem, but are “alternately” arranged, as no two stand at the same level. This, therefore, will be represented by \( \frac{1}{2} \), because in passing from one leaf to the next, an entire semicircle is traced, and from the second to the third another complete semicircle; so that the third leaf (which commences the next cycle) is over the first. This arrangement is consequently called distichous, as all the leaves on the stem will be in two vertical rows, and on opposite sides of the stem. In another kind, a cycle will coil thrice round the stem, and contain eight leaves; hence \( \frac{3}{8} \) will represent the angular divergence. Another is found to be \( \frac{1}{3} \), and several more exist.

8. If the fractions thus constructed from actual examination of plants be written down in succession according as the numerators and denominators increase, they will be seen to form a series with remarkable connections between its component fractions. It will be as follows: \( \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \frac{13}{34}, \frac{21}{55}, \frac{34}{89}, \ldots \); such I have elsewhere proposed to call the primary series. It cannot fail to be noticed that the sum of any two successive numerators, or of any two successive denominators, forms that of the next fraction respectively, so that we might extend this series indefinitely; thus: \( \frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \frac{13}{34}, \frac{21}{55}, \frac{34}{89}, \ldots \), &c. It will be also observed that the numerator of any fraction is the same num-

ber as the denominator next but one preceding it. There yet remains one more remarkable connection between them, viz., that these fractions are the successive convergents of the continued fraction

\[
\frac{1}{2 + \frac{1}{1 + \frac{1}{1 + \text{&c.}}}}
\]

That is to say, if we reduce, by the ordinary rules for simplifying fractions, the portions

\[
\frac{1}{2}, \frac{1}{2 + 1}, \frac{1}{2 + 1}, \frac{1}{1 + 1}, \frac{1}{1 + 1}
\]

and so on, the resulting fractions will be the same as those given above.

9. I have said that the above series of fractions represent the arrangements which exist in nature, and it is not usual to find any species departing from the arrangement which may be characteristic of it; in other words, the phyllotaxis of any species is constant to that species. The following are illustrations:

1. *Iris*, or Flag. The glumes (chaff) of all grasses. Some "orchids."

2. *Carex*, or Sedge. Leaves of several grasses.

3. Oak, Hawthorn. This is one of the commonest arrangements.


7. Hoary Plantain (*Plantago media*).

10. If, now, a semicircle be described, and one extremity of its diameter represent the position of any leaf, assumed as the first; and if a radius be drawn at the angular distance of 120° from this point, then the point where the radius meets the circumference will be the position of the second leaf of the tristichous arrangement. The opposite extremity of the diameter will be that of the second leaf of the distichous arrangement. And these points form the extreme positions for the second leaves of spirals of the primary series, corresponding to the fractions $\frac{1}{3}$ and $\frac{1}{4}$ respectively. No second leaf ever lies nearer to the first than 120°,
nor further than 180°.* The positions of all the second leaves are upon the arc included between those extreme points (viz., 120 and 180 degrees from the extremity of the diameter corresponding to the position of the assumed first leaf). Thus: for the pentastichous, as we have seen, it is at an angular distance of 144°; for the \( \frac{\pi}{4} \) divergence the second leaf is at an angular distance of 135°, while the positions of the second leaves of the spirals, represented by the consecutive fractions \( \frac{5}{6}, \frac{5}{7}, \frac{6}{7}, \frac{7}{8}, \) &c., gradually approximate to some intermediate point on the arc, but which no known example ever reaches. That point will be understood, by mathematicians, to represent the "limiting" value of the continued fraction \( \frac{1}{2} + \frac{1}{2 + 1} + \frac{1}{2 + 1 + 1} + \) \( \cdots \), or \( \frac{3 - \sqrt{5}}{2} \) of 360°, or 137° 30′ 28″.

11. Occasionally, other fractions must be constructed to indicate peculiar arrangements, and which cannot be represented by any one of the fractions of the primary series given above. I discovered the Jerusalem Artichoke to be a plant which, unlike most species having their own peculiar arrangements constantly the same, offered the most singular variety. Not only were some leaves opposite, i.e. in pairs at right angles, but also in threes, all on the same level; and when this was the case, they followed the same law regulating their positions, as already mentioned in the case of opposite or decussate leaves; viz., that the leaves of each group of three alternate in position with those of the groups above and below them; I have called† this arrangement tricussate. But besides these two kinds, the leaves on many stems were arranged alternately, and could be represented by the fractions \( \frac{1}{3}, \frac{2}{3}, \frac{3}{3}, \) &c. But more than this; for I found that the fractions \( \frac{3}{7}, \frac{3}{8}, \frac{7}{8}, \) &c. and others were likewise to be frequently obtained. Now these latter are obviously part of an analogous or secondary series; and if continued would stand thus: \( \frac{1}{3}, \frac{1}{4}, \frac{2}{3}, \frac{3}{7}, \frac{4}{8}, \frac{5}{8}, \frac{6}{2}, \) &c.

12. This secondary series will be seen, on comparing it with the primary, to differ in commencing with the fractions \( \frac{1}{3}, \frac{1}{4}, \) in place of \( \frac{1}{2}, \frac{1}{3}; \) but afterwards, each successive fraction may be written down as in the primary series by simply adding the two successive numerators and denominators respectively.

13. If, now, we project on a plane a cycle of any one of the spiral arrangements represented by a fraction of this secondary series, as in the case of \( \frac{1}{4}, \) we shall find that a complete circumference will invariably contain four leaves instead of

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* If the second leaf be at a greater distance than 180, and not less than 240 degrees from the first, it will be seen that the conditions are simply reversed, and the spiral will then run round in the opposite direction.
three. And, moreover, the angular divergence of any leaf from the next in succession will be found in a similar manner to be that fractional part of 360°. Similarly, just as all angular divergences of the leaves of the primary series lie between 120° and 180° inclusively, all those of the leaves of the secondary series lie between 90° and 120°; the limiting point being at an angular distance from the first leaf of 99° 30′ 6″+. Lastly, it must be observed that the fractions of the secondary series are the successive convergents of the continued fraction:

\[
\frac{1}{3} + \frac{1}{1+1+1+\cdots}
\]

14. In a manner analogous to the above, we might construct a tertiary series, commencing with the fractions \(\frac{1}{a}, \frac{1}{a+1}, \frac{2}{2a+1}, \frac{3}{3a+2}, \frac{5}{5a+3}, \&c\). Such a series, however, does not exist in nature, as far as I am aware. Having, then, before us three analogous series, it is obvious that we might construct any number of such series, and finally all would be represented by the algebraical forms, where \(a\) is any number:

\[
\frac{1}{a}, \frac{1}{a+1}, \frac{2}{2a+1}, \frac{3}{3a+2}, \frac{5}{5a+3}, \&c
\]

These fractions being the successive convergents of the continued fraction

\[
\frac{1}{a+1}, \frac{2}{2a+1+1}, \frac{3}{3a+2+1}, \frac{5}{5a+3+1}, \&c.
\]

15. In all the preceding investigations, I have supposed the space between any two successive leaves on the stem to have been sufficiently developed to enable me to trace an imaginary spiral line through the leaves. But it sometimes happens that such spaces, called *internodes*, are so short or are practically wanting, that the leaves become crowded together, so that it is quite impossible to say which is the second leaf after having fixed upon some one as the first. This is especially apparent in the case of fir-cones, where the scales may be considered as the representatives of leaves, and which, though crowded, are arranged in a strictly mathematical order.

16. If a cone of the Norway spruce fir be held vertically, the scales upon it will be observed to run in a series of parallel spirals, both to the left hand and to the right. This is a result of their being crowded together, as well as of their definite arrange-
ment. It is the object of the observer to detect and represent that order by some arithmetical symbol. This may be done by attending closely to the following directions:—Obs. 1. Fix upon any scale as No. 1, and mark the scale which lies in as nearly a vertical line over it as possible, viz., numbered at 22. Obs. 2. Note the scales which are below, nearest to, and overlap that scale (No. 22). Obs. 3. Run the eye along the two most elevated spirals, one to the right hand, the other to the left; and passing through these scales which overlap the scale numbered 22.* Obs. 4. Count the number of spirals (called secondary) which run round the cone parallel to these two spirals just observed; there will be found to be eight such parallel spirals to the right, and thirteen to the left, inclusive respectively of the two first noticed.

17. From these observations, a rule has been deduced for obtaining the fraction which represents the angular divergence of the so-called "generating" spiral which takes in every scale on the cone, in a manner similarly to those described above. Rule: The sum of the two numbers of parallel secondary spirals, viz. 13 + 8, or 21, forms the denominator, and the lowest, 8, supplies the numerator; so that \( \frac{8}{21} \) represents the angular divergence of the generating spiral. From this it is obvious that the scale immediately over No. 1 will be the 22nd, and this must commence a new cycle.

* These spirals are shaded in the figure so as to render them more conspicuous; viz., the spiral 1, 9, 17, 25, &c., to the right; and 1, 14, 27, 40, &c., to the left. I have said the most elevated spirals, because, had I chosen the spiral passing through the scales 1, 19, 37, 55, &c., or 1, 6, 11, 16, &c., the object of search would not have been obtained.
18. If the object of our search be only the discovery of this representative fraction \( \frac{a}{b} \), or the angular divergence of the generating spiral, then all that is required will have been done; but in order to prove the truth of the rule given above, we must proceed to affix numbers to every scale, and so put it to a rigid test. We have, then, to show that the first cycle of the spiral line passes through twenty-one scales before arriving at No. 22, which stands immediately over No. 1. Secondly, the cycle must coil eight times, or complete eight entire circumferences in so doing.

19. Method of Numbering the Scales.—Assuming there to have been 8 parallel secondary spirals to the right, and 13 to the left, as in fig. 2, the process of affixing a proper number to each scale on the cone is as follows:—Commencing with No. 1, affix the numbers 1, 9, 17, 25, 33, 41, 89, 97, 105, &c., on the scales of the secondary spiral passing through it to the right; these numbers being in arithmetical progression, the common difference being 8, or the number of such parallel spirals; thus all the scales on one of the secondary (as shaded) spirals will have numbers allotted to them. In a similar manner, affix the numbers 1, 14, 27, 40, 53, &c., on the successive scales of the secondary spiral to the left, using the common difference 13. Thus we shall have two secondary spirals intersecting at No. 1, and again at No. 105, with every scale properly numbered. From these two spirals all other scales can have proper numbers affixed to them. Thus, add 8 to the number of any scale, and affix the sum to the adjacent scale, on the right hand of it. Similarly, add 13 to the number of any scale, and affix the sum to the adjacent scale, on the left hand of it; e.g., if 8 be added to 40, 48 will be the number of the scale to the right of it, so that 40 and 48 are consecutive scales of a secondary spiral parallel to that passing through the scale 1, 9, 17, &c.; or if 13 be added to 25, 38 will be the number of the adjacent scale; i.e., on the spiral parallel to that passing through 1, 14, 27, &c. By this process, it will be easily seen that every scale on the cone can have a number assigned to it. When this has been done, if the cone be held vertically and caused to revolve, the observer can note the positions of each scale in order (1, 2, 3, 4, &c.) and he will then find that the cone will have revolved eight times before the eye will rest upon the 22nd scale, and which lies immediately over the first.

20. This experiment, then, proves the rule for the artificial method of discovering the fraction \( \frac{a}{b} \), which represents the angular divergence of the "generating" spiral.

21. We may also remember that there must be 21 vertical rows of leaves. These may generally be seen without much
difficulty by holding the cone horizontally, and looking parallel with its axis, when the twenty-one rows of vertical scales will be observed, somewhat in appearance like the rows of grains in a head of Indian corn.

22. I have said that the 22nd scale will be found immediately above, but not accurately in the same vertical line, with the one selected as No. 1. That it cannot be precisely so is obvious from the fact that \( \frac{22}{360} \) of 360°, or 137° 31' +, is not an aliquot part of a circumference; the consequence is, that the 22nd leaf must stand a little out of the vertical line, and of course the 43rd will be double that distance, and the 64th treble the amount, and so on. Hence it results that this supposed vertical line is in reality a highly-elevated spiral line, and instead of there being 21 actually vertical rows of scales, there will be 21 very elevated spirals (see fig. 2).

23. That the rows of leaves on any stem may be strictly vertical, the arrangement must be represented by some fraction the denominator of which measures 360°, such as \( \frac{1}{2}, \frac{1}{3}, \frac{2}{3}, \text{and} \frac{3}{4} \); whereas \( \frac{5}{8}, \frac{7}{11}, \&c. \), represent spirals in which no two leaves are ever in the same vertical line exactly.

24. As a general rule, all leaf-arrangements on stems with well-developed internodes can be represented by some one of the fractions \( \frac{1}{2}, \frac{1}{3}, \frac{2}{3}, \text{and} \frac{3}{4} \): whereas those with undeveloped internodes, as in the scales of cones, thistle-heads, &c., are represented by higher members of the series, such as \( \frac{5}{8}, \frac{7}{11}, \&c. \).

25. I must now turn to the other condition under which leaves are arranged, namely opposite. When this is the case, each pair of leaves, as has been stated above, stands at right angles to the pairs above and below it. Some plants have, either normally or occasionally, three or more leaves on the same level. When this is the case, the leaves of each group stand over the intervals of the group below it; \( i.e. \), they alternate with the leaves of the groups both above and below it.

26. This kind of arrangement is best seen in the parts of flowers, all of which are homologous with, or partake of, the same essential nature as leaves, and which, when complete in number, are separable into four sets of organs, called the four floral whorls; \( \text{viz.} \), calyx of sepals, corolla of petals, stamens, and pistil of carpels. It appears to be an invariable law that the parts of each whorl should alternate with those of the whorls above and below them. Indeed, so impressed are botanists with the persistency of this law, that when the parts of any one of the floral whorls stand immediately in front of the parts of a preceding external whorl, they at once infer that an intermediate whorl has disappeared. This is conspicuously the case in all primroses and cowslips, and other members of
the family to which they belong; wherein it will be noticed that each stamen is affixed or adherent to the tube of the corolla, but immediately in front of a petal, and not between two petals. That this idea of the suppression of another whorl of stamens is not without foundation, it may be observed that in the flowers of a little denizen of damp meadows, *Samolus Valerandi*, and akin to a primrose, has rudimentary stump-like organs which stand affixed to the corolla, and alternate with the petals; while the true stamens alternate with the former; and therefore, as in the Primrose, stand immediately in front of the petals. In the Primrose itself, no trace of any such suppressed whorl of stamens is ever apparent. In a large number of plants which are habitually—normally—without a corolla, the stamens, as would be expected, stand in front of, and not alternating with, the sepals.

27. Although the organs of flowers are usually grouped in distinct whorls, yet in many are they spirally arranged; and when this is the case, they can be represented by some fraction of the series given for alternate leaves.*

28. A point now to be particularly observed, is that these two arrangements, viz. the "spiral" and the "verticillate" (or "whorled," including the "opposite"), appear to be due to forces acting independently of each other; for it is rare to find whorls passing into spirals, and still rarer for spirals to pass into whorls—if, indeed, it ever occurs.

29. The Jerusalem Artichoke, however, furnishes many illustrations of the former process, and in some instances of the latter, though no gradual transition from a spiral to 'verticillate' or opposite conditions ever occurred in the cases examined.

30. A description of a few examples will be sufficient to enable it to be understood how a passage from opposite or verticillate leaves into spiral arrangements can be effected. Ex. I. The change from the opposite (decussate) leaves into the ¾ divergence. This occurred somewhat frequently as follows:—A pair of leaves slightly converge to one side, the angular distance between them being about 150°. The succeeding pair likewise converge, but have a somewhat less angle, one of the leaves in each case becoming slightly elevated by the development of an internode; so that the sixth leaf now appears over the first, or the lowest leaf of the first pair that converged to one side. It must be noted that the angles between the radii drawn to the position of the converging leaves do not accurately contain 144°,

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*A point worthy of note is, that the free portions of the corolla of a primrose overlap one another in just such a way as corresponds to the ¾ arrangement of spiral leaves; though, of course, they are actually verticillate.
or $\frac{2}{5} \times 360^\circ$. But as the spiral arrangement is continued up the stem and into the terminal bud, the leaves seem to "right" themselves, as it were; so that the appearance of the spiral in the neighbourhood of the summit is more accurate than at the point of departure from the highest pair of opposite leaves.

Ex. 2. Change from the tricussate arrangement into the $\frac{4}{5}$ divergence of the secondary series. A change from verticils of threes into the $\frac{4}{5}$ was frequent. It takes place in the following manner:—The first step is to cause the three leaves of the different whorls to separate slightly by a development of their internodes. Then, if any two consecutive whorls be examined, the order of succession of the six leaves (No. 1 being the lowest) is thus:

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6
3 7 9 2
4 8 5
1
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In which it will be noticed that the fourth leaf, instead of being over the interval between the first and second, is over that between the third and first, so that the angle between the first and second leaf, or between the second and third, is double that between the third and fourth. These latter, it will be remembered, are separated by a long internode. The same order obtains with the succeeding whorls; the nodes, however, are now much more widely separated, while a true spiral arrangement, with the same angular distance between all its leaves, is ultimately secured, and is henceforth continued uninterruptedly into the terminal bud, and represented by the fraction $\frac{4}{7}$.

31. From very many observations on stems of the Jerusalem Artichoke, it appears that to resolve opposite and decussate leaves into spirals of the primary series and tricussate verticils into those of the secondary series is more easily accomplished than any other kinds of transition. To reverse the process, or to bring back spirals into verticils, seems quite contrary to all nature's tendencies to change. Stems of the Jerusalem Artichoke occasionally had their leaves arranged spirally below, and verticillate above; but then the change was abrupt. The spiral suddenly terminated, and the last leaf was succeeded by three in a whorl.

Conclusion.—I have now endeavoured to give a brief and as clear account as I can of the main facts and principles of Phyllotaxis. But, if we venture to search for a cause of such definite and exact arrangements of leaves, it will probably be fruitless, for as yet no satisfactory explanation has ever been given. It is not enough to say that it is a wise arrangement that leaves should not all be over one another, so as to exclude
the light and air, and impede each other’s functions; or that the alternate arrangement is an obviously wise method of securing a larger development of “blade” and conditions equally favourable to all. Nevertheless, it is fact that when leaves are crowded, or verticillate, they very often appear less capable of sustaining much development of surface.* But this might presumably have been attained without the strictly mathematical positions which alternate leaves have assigned to them.

We may, then, ask two questions, both of which are at present unanswerable. First, why does a leaf of any spiral amongst ordinary plants stand at an angular distance varying from 120° to 180° from the next to it on the stem? Secondly, why does it take up an accurate or definite position on the arc between those limits, and is not to be found anywhere along that arc?

All that can be said is, that such is the case in nature, and that when the angles between any two successive leaves of all the different generating spirals are measured, and represented as fractional parts of the circumference, they are found to bear such relations to one another when written down in succession, as obtain between the successive convergents of a continued fraction of the general form: \(-\frac{1}{a + \frac{1}{1 + \frac{1}{1 + \text{&c.}}}}\).

Whatever our speculations, as to the cause of Phyllotaxis, may be, the fact nevertheless remains, and, like the beautiful structure of the bee-cell, testifies to the truth that “God’s ways are past finding out,” though bearing witness the while by its general invariability to the prevalence of law, and by its exactness and functional value to the power and wisdom of the Law-Giver.

A discussion ensued, in which Mr. J. Reddie, Mr. A. V. Newton, the Rev. C. A. Row, Dr. J. A. Fraser, Mr. Hubert Airy, and the Chairman took part: the Rev. G. Henslow replied.

The Meeting was then adjourned.

* e.g. The “orders” Coniferae, Galiaceae, and in the genera Hippuris, Myriophyllum, and Callitriche.