PROBLEMS OF HEREDITY AS A SUBJECT FOR HORTICULTURAL INVESTIGATION.

BY MR. W. BATESON, M.A., F.R.S.

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May 8, 1900

Mendel's work from 1865 was largely neglected, until 1900 when it was simultaneously rediscovered by Hugo de Vries, Carl Correns, and Erik von Tschermak. When Mendel's work came to the attention of William Bateson (who himself had already been advocating controlled crosses as an approach to studying heredity), he was convinced that Mendel's work was of major importance:

That we are in the presence of a new principle of the highest importance is, I think, manifest. To what further conclusions it may lead us cannot yet be foretold. (This paper, p. 9)

Bateson devoted his scientific career to further elucidations of "Mendelism." This present paper captures the enthusiasm of his first encounter with the works of Mendel.

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AN EXACT DETERMINATION OF THE LAWS OF HEREDITY will probably work more change in man's outlook on the world, and in his power over nature, than any other advance in natural knowledge that can be foreseen.

There is no doubt whatever that these laws can be determined. In comparison with the labour that has been needed for other great discoveries it is even likely that the necessary effort will be small. It is rather remarkable that while in other branches of physiology such great progress has of late been made, our knowledge of the phenomena of heredity has increased but little; though that these phenomena constitute the basis of all evolutionary science and the very central problem of natural history is admitted by all. Nor is this due to the special difficulty of such inquiries so much as to general neglect of the subject.

It is in the hope of inducing others to pursue these lines of investigation that I take the problems of heredity as the subject of this lecture to the Royal Horticultural Society.

No one has better opportunities of pursuing such work than horticulturists. They are daily witnesses of the phenomena of heredity. Their success depends also largely on a knowledge of its laws, and obviously every increase in that knowledge is of direct and special importance to them.

The want of systematic study of heredity is due chiefly to misapprehension. It is supposed that such work requires a lifetime.

But though for adequate study of the complex phenomena of inheritance long periods of time must be necessary, yet in our present state of deep ignorance almost of the outline of the facts, observations carefully planned and faithfully carried out for even a few years may produce results of great value. In fact, by far the most appreciable and definite additions to our knowledge of these matters have been thus obtained.

There is besides some misapprehension as to the kind of knowledge which is especially wanted at this time, and as to the modes by which we may expect to obtain it. The present paper is written in the hope that it may in some degree help to clear the ground of these difficulties by a preliminary consideration of the question. How far have we got towards an exact knowledge of heredity, and how can we get further?

Now this is pre-eminently a subject in which we must distinguish what we *can* do from what we want to do. We *want* to know the whole truth of the matter; we want to know the physical basis, the inward and essential nature, "the causes," as they are sometimes called, of heredity. We want also to know the laws which the outward and visible phenomena obey.

Let us recognise from the outset that as to the essential nature of these phenomena we still know absolutely nothing. We have no glimmering of an idea as to what constitutes the essential process by which the likeness of the parent is transmitted to the offspring. We can study the processes of fertilisation and development in the finest detail which the microscope manifests to us, and we may fairly say that we have now a thorough grasp of the visible phenomena; but of the nature of the physical basis of heredity we have no conception at all. No one has yet any suggestion, working hypothesis, or mental picture that has thus far helped in the slightest degree to penetrate beyond what we see. The process is as utterly mysterious to us as a flash of lightning is to a savage. We do not know what is the essential agent in the transmission of parental characters, not even whether it is a material agent or not. Not only is our ignorance complete, but no one has the remotest idea how to set to work on that part of the problem. We are in the state in which the students of physical science were in the period when it was open to anyone to believe that heat was a material substance or not, as he chose.

But apart from any conception of the essential modes of transmission of characters, we can study the outward facts of the transmission. Here, if our knowledge is still very vague, we are at least beginning to see how we ought to go to work. Formerly

naturalists were content with the collection of numbers of isolated instances of transmission—more especially, striking and peculiar cases—the sudden appearance of highly prepotent forms, and the like. We are now passing out of that stage. It is not that the interest of particular cases has in any way diminished—for such records will always have their value—but it has become likely that general expressions will be found capable of sufficiently wide application to be justly called "laws" of heredity. That this is so is due almost entirely to the work of Mr. F. Galton, to whom we are indebted for the first systematic attempt to enunciate such a law.

All laws of heredity so far propounded are of a statistical character and have been obtained by statistical methods. If we consider for a moment what is actually meant by a "law of heredity" we shall see at once why these investigations must follow statistical methods. For a "law" of heredity is simply an attempt to declare the course of heredity under given conditions. But if we attempt to predicate the course of heredity we have to deal with conditions and groups of causes wholly unknown to us, whose presence we cannot recognise, and whose magnitude we cannot estimate in any particular case. The course of heredity in particular cases therefore cannot be foreseen.

Of the many factors which determine the degree to which a given character shall be present in a given individual only one is known to us, namely, the degree to which that character is present in the parents. It is common knowledge that there is not that close correspondence between parent and offspring which would result were this factor the only one operating; but that, on the contrary, the resemblance between the two is only a general one.

In dealing with phenomena of this class the study of single instances reveals no regularity. It is only by collection of facts in great numbers, and by statistical treatment of the mass, that any order or law can be perceived. In the case of a chemical reaction, for instance, by suitable means the conditions can be accurately reproduced, so that in every individual case we can predict with certainty that the same result will occur. But with heredity it is somewhat as it is in the case of the rainfall. No one can say how much rain will fall to-morrow in a given place, but we can predict with moderate accuracy how much will fall next year, and for a period of years a prediction can be made which accords very closely with the truth.

Similar predictions can from statistical data be made as to the duration of life and a great variety of events the conditioning causes of which are very imperfectly understood. It is predictions of this kind

that the study of heredity is beginning to make possible, and in that sense laws of heredity can be perceived.

We are as far as ever from knowing why some characters are transmitted, while others are not; nor can anyone yet foretell which individual parent will transmit characters to the offspring, and which will not; nevertheless the progress made is distinct.

As yet investigations of this kind have been made in only a few instances, the most notable being those of Galton on human stature, and on the transmission of colours in Basset hounds. In each of these cases he has shown that the expectation of inheritance is such that a simple arithmetical rule is approximately followed. The rule thus arrived at is that of the whole heritage of the offspring the two parents together on an average contribute one half, the four grandparents one quarter, the eight great-grandparents one eighth, and so on, the remainder being contributed by the remoter ancestors.

Such a law is obviously of practical importance. In any case to which it applies we ought thus to be able to predict the degree with which the purity of a strain may be increased by selection in each successive generation.

To take a perhaps impossibly crude example, if a seedling show any particular character which it is desired to fix, on the assumption that successive self-fertilisations are possible, according to Galton's law the expectation of purity should be in the first generation of self-fertilisation 1 in 2, in the second generation 3 in 4, in the third 7 in 8, and so on.

But already many cases are known to which the rule in the simple form will not apply. Galton points out that it takes no account of individual prepotencies. There are, besides, numerous cases in which on crossing two varieties the character of one variety is almost always transmitted to the first generation. Examples of these will be familiar to those who have experience in such matters. The offspring of the Polled Angus cow and the Shorthorn bull is almost invariably polled. Seedlings raised by crossing *Atropa belladonna* with the yellow-fruited variety have without exception the blackish-purple fruits of the type. In several hairy species when a cross with a glabrous variety is made, the first cross-bred generation is altogether hairy.

Still more numerous are examples in which the characters of one variety very largely, though not exclusively, predominate in the offspring.

These large classes of exception—to go no further—indicate that, as we might in any case expect, the principle is not of universal

application, and will need various modifications if it is to be extended to more complex cases of inheritance of varietal characters. No more useful work can be imagined than a systematic determination of the precise "law of heredity" in numbers of particular cases.

Until lately the work which Galton accomplished stood almost alone in this field, but quite recently remarkable additions to our knowledge of these questions have been made. In the present year Professor de Vries published a brief account[1] of experiments which he has for several years been carrying on, giving results of the highest value.

The description is very short, and there are several points as to which more precise information is necessary both as to details of procedure and as to statement of results.[2] Nevertheless it is impossible to doubt that the work as a whole constitutes a marked step forward, and the full publication which is promised will be awaited with great interest.

The work relates to the course of heredity in cases where definite varieties differing from each other in some *one* definite character are crossed together. The cases are all examples of discontinuous variation: that is to say, cases in which actual intermediates between the parent forms are not usually produced on crossing. It is shown that the subsequent posterity obtained by self-fertilising these cross-breds or hybrids break up into the original parent according to fixed numerical rule.

Professor de Vries begins by reference to a remarkable memoir by Gregor Mendel,[3] giving the results of his experiments in crossing varieties of *Pisum sativum.* These experiments of Mendel's were carried out on a large scale, his account of them is excellent and complete, and the principles which he was able to deduce from them will certainly play a conspicuous part in all future discussions of evolutionary problems. It is not a little remarkable that Mendel's work should have escaped notice, and been so long forgotten.

For the purposes of his experiments Mendel selected seven pairs of characters as follows:—

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[1]   *Comptes Rendus*, March 26, 1900, and *Ber. d. Deutsch. Bot. Ges.,* xviii. 1900, p. 83.

[2]   For example, I do not understand in what sense de Vries considers that Mendel's law can be supposed to apply even to all "monohybrids," for numerous cases are already known in which no such rule is obeyed.

[3]   'Versuche üb. Pflanzenhybriden' in the Verh. d. Naturf. Ver. Brünn, iv. 1865.

1. Shape of ripe seed, whether round, or angular and wrinkled.

2. Colour of "endosperm" (cotyledons), whether some shade of yellow, or a more or less intense green.

3. Colour of the seed-skin, whether various shades of grey and gray-brown, or white.

4. Shape of seed-pod, whether simply inflated, or deeply constricted between the seeds.

5. Colour of unripe pod, whether a shade of green, or bright yellow.

6. Shape of inflorescence, whether the flowers are arranged along on axis, or are terminal and more or less umbellate.

7. Length of peduncle, whether about 6 or 7 inches long, or about ¾ to 1½ inch.

Large numbers of crosses were made between Peas differing in respect of each of these pairs of characters. It was found that in each case the offspring of the cross exhibited the character of one of the parents in almost undiminished intensity, and intermediates which could not be at once referred to one or other of the parental forms were not found.

In the case of each pair of characters there is thus one which in the first cross prevails to the exclusion of the other. This prevailing character Mendel calls the *dominant* character, the other being the *recessive* character.[4]

That the existence of such "dominant" and "recessive" characters is a frequent phenomenon in cross-breeding, is well known to all who have attended to these subjects.

By self-fertilising the cross-breds Mendel next raised another generation. In this generation were individuals which showed the dominant character, but also individuals which preserved the recessive character. This fact also is known in a good many instances. But Mendel discovered that in this generation the numerical proportion of dominants to recessives is approximately constant, being in fact *as three to one*. With very considerable regularity these numbers were approached in the case of each of his pairs of characters.

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4   Note that by these useful terms the complications involved by use of the expression "prepotent" are avoided.

There are thus in the first generation raised from the cross-breds 75 per cent. dominants and 25 per cent. recessives.

These plants were again self-fertilised, and the offspring of each plant separately sown. It next appeared that the offspring of the recessives *remained pure recessive,* and in subsequent generations never reverted to the dominant again.

But when the seeds obtained by self-fertilising the dominants were sown it was found that some of the dominants gave rise to pure dominants, while others had a mixed offspring, composed partly of recessives, partly of dominants. Here also it was found that the average numerical proportions were constant, those with pure dominant offspring being to those with mixed offspring as one to two. Hence it is seen that the 75 per cent. dominants really are not all alike, but consist of twenty-five which are pure dominants and fifty which are really cross-breds, though, like the cross-breds raised by crossing the two varieties, they only exhibit the dominant character.

To resume, then, it was found that by self-fertilising the original cross-breds the same proportion was always approached, namely—

25 dominants, 50 cross-breds, 25 recessives, or 1D : 2DR : 1R.

Like the pure recessives, the pure dominants are thenceforth pure, and only give rise to dominants in all succeeding generations.

On the contrary the fifty cross-breds, as stated above, have mixed offspring. But these, again, in their numerical proportions, follow the same law, namely, that there are three dominants to one recessive. The recessives are pure like those of the last generation, but the dominants can, by further self-fertilisation and cultivation of the seeds produced, be shown to be made up of pure dominants and cross-breds in the same proportion of one dominant to two cross-breds.

The process of breaking up into the parent forms is thus continued in each successive generation, the same numerical law being followed so far as has yet been observed.

Mendel made further experiments with *Pisum sativum,* crossing pairs of varieties which differed from each other in *two* characters, and the results, though necessarily much more complex, showed that the law exhibited in the simpler case of pairs differing in respect of one character operated here also.

Professor de Vries has worked at the same problem in some dozen species belonging to several genera, using pairs of varieties characterised by a great number of characters: for instance, colour of flowers, stems, or fruits, hairiness, length of style, and so forth. He states that in all these cases Mendel's law is followed.

The numbers with which Mendel worked, though large, were not large enough to give really smooth results; but with a few rather marked exceptions the observations are remarkably consistent, and the approximation to the numbers demanded by the law is greatest in those cases where the largest numbers were used. When we consider, besides, that Tschermak and Correns announce definite confirmation in the case of *Pisum,* and de Vries adds the evidence of his long series of observations on other species and orders, there can be no doubt that Mendel's law is a substantial reality; though whether some of the cases that depart most widely from it can be brought within the terms of the same principle or not, can only be decided by further experiments.

One may naturally ask, How can these results be brought into harmony with the facts of hybridisation as hitherto known; and, if all this is true, how is it that others who have so long studied the phenomena of hybridisation have not long ago perceived this law? The answer to this question is given by Mendel at some length, and it is, I think, satisfactory. He admits from the first that there are undoubtedly cases of hybrids and cross-breds which maintain themselves pure and do not break up. Such examples are plainly outside the scope of his law. Next he points out, what to anyone who has rightly comprehended the nature of discontinuity in variation is well known, that the variations in *each* character must be *separately* regarded. In most experiments in crossing, forms are taken which differ from each other in a multitude of characters—some continuous, others discontinuous, some capable of blending with their contraries, while others are not. The observer on attempting to perceive any regularity is confused by the complications thus introduced. Mendel's law, as he fairly says, could only appear in such cases by the use of overwhelming numbers, which are beyond the possibilities of practical experiment.

Both these answers should be acceptable to those who have studied the facts of variation and have appreciated the nature of Species in the light of those facts. That different species should follow different laws, and that the same law should not apply to all characters alike, is exactly what we have every right to expect. It will also be remembered that the principle is only declared to apply to discontinuous characters. As stated also it can only be true where reciprocal crossings lead to the same result. Moreover, it can only be tested when there is no sensible diminution in fertility on crossing.

Upon the appearance of de Vries' papers announcing the "rediscovery" and confirmation of Mendel's law and its extension to a

great number of cases two other observers came forward and independently describe series of experiments fully confirming Mendel's work. Of these papers the first is that of Correns,[5] who repeated Mendel's original experiment with Peas having seeds of different colours. The second is a long and very valuable memoir of Tschermak,[6] which gives an account of elaborate researches into the results of crossing a number of varieties of *Pisum sativum*. These experiments were in many cases carried out on a large scale, and prove the main fact enunciated by Mendel beyond any possibility of contradiction. Both Correns (in regard to Maize) and Tschermak in the case of *P. sativum* have obtained further proof that Mendel's law holds as well in the case of varieties differing from each other in *two* characters, one of each being dominant, though of course a more complicated expression is needed in such cases.[7]

That we are in the presence of a new principle of the highest importance is, I think, manifest. To what further conclusions it may lead us cannot yet be foretold. But both Mendel and the authors who have followed him lay stress on one conclusion, which will at once suggest itself to anyone who reflects on the facts. For it will be seen that the results are such as we might expect if it is imagined that the cross-bred plant produced pollen grains and ovules, each of which bears only one of the alternative varietal characters and not both. If this were so, and if on the average the same number of pollen grains and ovules partook of each of the two characters, it is clear that on a random assortment of pollen grain and ovules Mendel's law would be obeyed. For 25 per cent. of "dominant" pollen grains would unite with 25 per cent. "dominant" ovules; 25 per cent. "recessive" pollen grains would similarly unite with 25 per cent. "recessive" ovules; while the remaining 50 per cent. of each kind would unite together. It is this consideration which leads both de Vries and Mendel to assert that these facts of crossing prove that each ovule and each pollen grain is pure in respect of each character to which the law applies. It is highly desirable that varieties differing in the form of their pollen should be made the subject of these experiments, for it is quite possible that in such a case strong confirmation of this deduction might be obtained.

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[5]   Ber. *deut. Bot. Ges.,* 1900, xviii. p. 158.

[6]   *Zeitschr. f. d. landw.* Versuchswesen in Oesterr., 1900, iii. p. 465.

[7]   Tschermak's investigations were besides directed to a re-examination of the question of the absence of beneficial results on cross-fertilising *P. sativum*, a subject already much investigated by Darwin, and upon this matter also important further evidence is given in great detail.

As an objection to this deduction, however, it is to be noted that though true intermediates did not occur, yet the degrees in which the characters appeared did vary in degree, and it is not easy to see how the hypothesis of perfect purity in the reproductive cells can be supported in such cases. Be this, however, as it may, there is no doubt we are beginning to get new lights of a most valuable kind on the nature of heredity and the laws which it obeys. It is to be hoped that these indications will be at once followed up by independent workers. Enough has been said to show how necessary it is that the subjects of experiment should be chosen in such a way as to bring the laws of heredity to a real test. For this purpose the first essential is that the differentiating characters should be few, and that all avoidable complications should be got rid of. Each experiment should be reduced to its simplest possible limits. The results obtained by Galton, and also the new ones especially detailed in this paper' have each been reached by restricting the range of observation to one character or group of characters, and there is every hope that by similar treatment our knowledge of heredity may be rapidly extended.

[Note. -- Since the above was printed further papers on Mendel's Law have appeared, namely, de Vries, *Rev. génér. Bot.,* 1900, p. 257; Correns, *Bot. Ztg.,* 1900, p. 229; and *Bot. Cblt.*, lxxxiv., p. 97, containing new matter of importance. Prof. de Vries kindly writes to me that in asserting the general applicability of Mendel's Law to "monohybrids" (crosses between parents differing in respect of one character only), he intends to include eases of discontinuous varieties only, and he does not mean to refer to continuous varieties at all. (October 31, 1900.]