THE PROBLEMS OF HEREDITY AND THEIR SOLUTION*.

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 clearly 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 we may even expect 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.

* The first half of this paper is reprinted with additions and modifications from the Journal of the Royal Horticultural Society, 1900, vol. xxv., parts 1 and 2. Written almost immediately after the rediscovery of Mendel, it will be seen to be already in some measure out of date, but it may thus serve to show the relation of the new conceptions to the old.

B.
2

The Problems

It is in the hope of inducing others to follow 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 and stock breeders. They are daily witnesses of the phenomena of heredity. Their success also depends 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
of Heredity

essential nature, “the causes,” as they are sometimes called, of heredity: but 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 considerable 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
The Problems

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 was till recently 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 recognize, 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 usually 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 an uncertain one.

In dealing with phenomena of this class the study
of Heredity

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
The Problems

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 any 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 almost always appears in each member of the first cross-bred 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 or with very small loose “scurs.” Seedlings raised by crossing *Atropa belladonna* with the yellow-fruit 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, pre-dominate in the offspring.


† These we now recognize as examples of Mendelian ‘dominance.’
of Heredity

These large classes of exceptions—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 year 1900 Professor de Vries published a brief account* 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. 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, or by breeding them with each other, break up into the original parent forms according to fixed numerical rule.


† This conception of discontinuity is of course pre-Mendelian.
8

The Problems

Professor de Vries begins by reference to a remarkable memoir by Gregor Mendel*, 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:—

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 grey-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. Nature of inflorescence, whether the flowers are arranged along the axis of the plant; or are terminal and form a kind of umbel.

7. Length of stem, whether about 6 or 7 ft. long, or about 3/4 to 1 1/2 ft.

Large numbers of crosses were made between Peas differing in respect of one of each of these pairs of characters.

of Heredity

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*.

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 letting the cross-breds fertilise themselves Mendel next raised another generation. In this generation were individuals which showed the dominant character, but also individuals which presented the recessive character. Such a fact also was known in a good many instances. But Mendel discovered that in this generation the numerical proportion of dominants to recessives is on an average of cases 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.

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 produced the dominant again.

But when the seeds obtained by self-fertilising the

* Note that by these novel terms the complications involved by use of the expression “prepotent” are avoided.
The Problems

dominants were examined and sown it was found that the dominants were not all alike, but consisted of two classes, (1) those which gave rise to pure dominants, and (2) others which gave 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 are not really of similar constitution, 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 original 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 studied.

On the contrary the fifty cross-breds, as stated above, have mixed offspring. But these offspring, 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 examination or cultivation of the seeds produced, be again 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