A DEFENCE OF MENDEL'S PRINCIPLES OF HEREDITY.

"*The most fertile men of science have made blunders, and their consciousness of such slips has been retribution enough; it is only their more sterile critics who delight to dwell too often and too long on such mistakes.*" BIOMETRIKA, 1901.

INTRODUCTORY.

ON the rediscovery and confirmation of Mendel's Law by de Vries, Correns, and Tschermak two years ago, it became clear to many naturalists, as it certainly is to me, that we had found a principle which is destined to play a part in the Study of Evolution comparable only with the achievement of Darwin—that after the weary halt of forty years we have at last begun to march.

If we look back on the post-Darwinian period we recognize one notable effort to advance. This effort—fruitful as it proved, memorable as it must ever be—was that made by Galton when he enuntiated his Law of Ancestral Heredity, subsequently modified and restated by Karl Pearson. Formulated after long and laborious inquiry, this principle beyond question gives us an expression including and denoting many phenomena in which previously no regularity had been detected. But

to practical naturalists it was evident from the first that there are great groups of facts which could not on any interpretation be brought within the scope of Galton's Law, and that by no emendation could that Law be extended to reach them. The existence of these phenomena pointed to a different physiological conception of heredity. Now it is precisely this conception that Mendel's Law enables us to form. Whether the Mendelian principle can be extended so as to include some apparently Galtonian cases is another question, respecting which we have as yet no facts to guide us, but we have certainly no warrant for declaring such an extension to be impossible.

Whatever answer the future may give to that question, it is clear from this moment that every case which obeys the Mendelian principle is removed finally and irretrievably from the operations of the Law of Ancestral Heredity.

At this juncture Professor Weldon intervenes as a professed exponent of Mendel's work. It is not perhaps to a devoted partisan of the Law of Ancestral Heredity that we should look for the most appreciative exposition of Mendel, but some bare measure of care and accuracy in representation is demanded no less in justice to fine work, than by the gravity of the issue.

Professor Weldon's article appears in the current number of *Biometrika*, Vol. I. Pt. II. which reached me on Saturday, Feb. 8. The paper opens with what purports to be a restatement of Mendel's experiments and results. In this "restatement" a large part of Mendel's experiments—perhaps the most significant—are not referred to at all. The perfect simplicity and precision of Mendel's own account are destroyed; with the result that the reader of Professor Weldon's paper, unfamiliar with Mendel's own memoir, can scarcely be blamed if he fail to learn the

essence of the discovery. Of Mendel's conception of the hybrid as a distinct entity with characters proper to itself, apart from inheritance—the most novel thing in the whole paper—Professor Weldon gives no word. Upon this is poured an undigested mass of miscellaneous "facts" and statements from which the reader is asked to conclude, first, that a proposition attributed to Mendel regarding dominance of one character is not of "general"* application, and finally that "all work based on Mendel's method" is "vitiated" by a "fundamental mistake," namely "the neglect of ancestry†."

To find a parallel for such treatment of a great theme in biology we must go back to those writings of the orthodox which followed the appearance of the "Origin of Species."

On 17th December 1900 I delivered a Report to the Evolution Committee of the Royal Society on the experiments in Heredity undertaken by Miss E. R. Saunders and myself. This report has been offered to the Society for publication and will I understand shortly appear. In it we have attempted to show the extraordinary significance of Mendel's principle, to point out what in his results is essential and what subordinate, the ways in which the principle can be extended to apply to a diversity of more complex phenomena—of which some are incautiously cited

* The words "general" and "universal" appear to be used by Professor Weldon as interchangeable. Cp. Weldon, p. 235 and elsewhere, with Abstract given below.

† These words occur p. 252: "The fundamental mistake which vitiates all work based upon Mendel's method is the neglect of ancestry, and the attempt to regard the whole effect upon offspring produced by a particular parent, as due to the existence in the parent of particular structural characters, &c." As a matter of fact the view indicated in these last words is especially repugnant to the Mendelian principle, as will be seen.

by Professor Weldon as conflicting facts—and lastly to suggest a few simple terms without which (or some equivalents) the discussion of such phenomena is difficult. Though it is impossible here to give an outline of facts and reasoning there set out at length, I feel that his article needs an immediate reply. Professor Weldon is credited with exceptional familiarity with these topics, and his paper is likely to be accepted as a sufficient statement of the case. Its value will only be known to those who have either worked in these fields themselves or have been at the trouble of thoughtfully studying the original materials.

The nature of Professor Weldon's article may be most readily indicated if I quote the summary of it issued in a paper of abstracts sent out with Review copies of the Part. This paper was most courteously sent to me by an editor of *Biometrika* in order to call my attention to the article on Mendel, a subject in which he knew me to be interested. The abstract is as follows.

"Few subjects have excited so much interest in the last year or two as the laws of inheritance in hybrids. Professor W. F. R. Weldon describes the results obtained by Mendel by crossing races of Peas which differed in one or more of seven characters. From a study of the work of other observers, and from examination of the 'Telephone' group of hybrids, the conclusion is drawn that Mendel's results do not justify any general statement concerning inheritance in cross-bred Peas. A few striking cases of other cross-bred plants and animals are quoted to show that the results of crossing cannot, as Mendel and his followers suggest, be predicted from a knowledge of the characters of the two parents crossed without knowledge of the more remote ancestry."

Such is the judgment a fellow-student passes on this mind

"*Voyaging through strange seas of thought alone.*"

The only conclusion which most readers could draw from this abstract and indeed from the article it epitomizes, is that Mendel's discovery so far from being of paramount importance, rests on a basis which Professor Weldon has shown to be insecure, and that an error has come in through disregard of the law of Ancestral Heredity. On examining the paper it is perfectly true that Professor Weldon is careful nowhere directly to question Mendel's facts or his interpretation of them, for which indeed in some places he even expresses a mild enthusiasm, but there is no mistaking the general purpose of the paper. It must inevitably produce the impression that the importance of the work has been greatly exaggerated and that supporters of current views on Ancestry may reassure themselves. That this is Professor Weldon's own conclusion in the matter is obvious. After close study of his article it is evident to me that Professor Weldon's criticism is baseless and for the most part irrelevant, and I am strong in the conviction that the cause which will sustain damage from this debate is not that of Mendel.

I. The Mendelian Principle of Purity of Germ-Cells and the Laws of Heredity based on Ancestry.

Professor Weldon's article is entitled "Mendel's Laws of Alternative Inheritance in Peas." This title expresses the scope of Mendel's work and discovery none too precisely and even exposes him to distinct misconception.

To begin with, it says both too little and too much. Mendel did certainly determine Laws of Inheritance in

peas—not precisely the laws Professor Weldon has been at the pains of drafting, but of that anon. Having done so, he knew what his discovery was worth. He saw, and rightly, that he had found a principle which *must* govern a wide area of phenomena. He entitles his paper therefore "*Versuche über Pflanzen-Hybriden*," or, Experiments in Plant-Hybridisation.

Nor did Mendel start at first with any particular intention respecting Peas. He tells us himself that he wanted to find the laws of inheritance in *hybrids*, which he suspected were definite, and that after casting about for a suitable subject, he found one in peas, for the reasons he sets out.

In another respect the question of title is much more important. By the introduction of the word "Alternative" the suggestion is made that the Mendelian principle applies peculiarly to cases of "alternative" inheritance. Mendel himself makes no such limitation in his earlier paper, though perhaps by rather remote implication in the second, to which the reader should have been referred. On the contrary, he wisely abstains from prejudicial consideration of unexplored phenomena.

To understand the significance of the word "alternative" as introduced by Professor Weldon we must go back a little in the history of these studies. In the year 1897 Galton formally announced the Law of Ancestral Heredity referred to in the *Introduction*, having previously "stated it briefly and with hesitation" in *Natural Inheritance*, p. 134. In 1898 Professor Pearson published his modification and generalisation of Galton's Law, introducing a correction of admitted theoretical importance, though it is not in question that the principle thus restated is funda-

mentally not very different from Galton's*. *It is an essential part of the Galton-Pearson Law of Ancestral Heredity that in calculating the probable structure of each descendant the structure of each several ancestor must be brought to account.*

Professor Weldon now tells us that these two papers of Galton and of Professor Pearson have "given us an expression for the effects of *blended* inheritance which seems likely to prove generally applicable, though the constants of the equations which express the relation between divergence from the mean in one generation, and that in another, may require modification in special cases. Our knowledge of *particulate* or mosaic inheritance, and of *alternative* inheritance, is however still rudimentary, and there is so much contradiction between the results obtained by different observers, that the evidence available is difficult to appreciate."

But Galton stated (p. 401) in 1897 that his statistical law of heredity "appears to be universally applicable to bi-sexual descent." Pearson in re-formulating the principle in 1898 made no reservation in regard to "alternative" inheritance. On the contrary he writes (p. 393) that "if Mr Galton's law can be firmly established, *it is a complete solution, at any rate to a first approximation, of the whole problem of heredity*," and again (p. 412) that "it is highly probable that it [this law] is the simple descriptive state-

* I greatly regret that I have not a precise understanding of the basis of the modification proposed by Pearson. His treatment is in algebraical form and beyond me. Nevertheless I have every confidence that the arguments are good and the conclusion sound. I trust it may not be impossible for him to provide the non-mathematical reader with a paraphrase of his memoir. The arithmetical differences between the original and the modified law are of course clear.

ment which brings into a single focus all the complex lines of hereditary influence. If Darwinian evolution be natural selection combined with *heredity*, then the single statement which embraces the whole field of heredity must prove almost as epoch-making as the law of gravitation to the astronomer*."

As I read there comes into my mind that other fine passage where Professor Pearson warns us

> "There is an insatiable desire in the human breast
> "to resume in some short formula, some brief
> "statement, the facts of human experience. It leads
> "the savage to 'account' for all natural phenomena
> "by deifying the wind and the stream and the tree.
> "It leads civilized man, on the other hand, to express
> "his emotional experience in works of art, and his
> "physical and mental experience in the formulae or
> "so-called laws of science†."

No naturalist who had read Galton's paper and had tried to apply it to the facts he knew could fail to see that here was a definite advance. We could all perceive phenomena that were in accord with it and there was no reasonable doubt that closer study would prove that accord to be close. It was indeed an occasion for enthusiasm, though no one acquainted with the facts of experimental breeding could consider the suggestion of universal application for an instant.

* I have searched Professor Pearson's paper in vain for any considerable reservation regarding or modification of this general statement. Professor Pearson enuntiates the law as "only correct on certain limiting hypotheses," but he declares that of these the most important is "the absence of reproductive selection, i.e. the negligible correlation of fertility with the inherited character, and the absence of sexual selection." The case of in-and-in breeding is also reserved.

† K. Pearson, *Grammar of Science*, 2nd ed. 1900, p. 36.

But two years have gone by, and in 1900 Pearson writes* that the values obtained from the Law of Ancestral Heredity

> "seem to fit the observed facts fairly well in the case of "*blended* inheritance. In other words we have a "certain amount of evidence in favour of the "conclusion: *That whenever the sexes are equipotent,* "*blend their characters and mate pangamously, all* "*characters will be inherited at the same rate,*"

or, again in other words, that the Law of Ancestral Heredity after the glorious launch in 1898 has been home for a complete refit. The top-hamper is cut down and the vessel altogether more manageable; indeed she looks trimmed for most weathers. Each of the qualifications now introduced wards off whole classes of dangers. Later on (pp. 487—8) Pearson recites a further list of cases regarded as exceptional. "All characters will be inherited at the same rate" might indeed almost be taken to cover the results in Mendelian cases, though the mode by which those results are arrived at is of course wholly different.

Clearly we cannot speak of the Law of Gravitation now. Our Tycho Brahe and our Kepler, with the yet more distant Newton, are appropriately named as yet to come†.

But the truth is that even in 1898 such a comparison was scarcely happy. Not to mention moderns, these high hopes had been finally disposed of by the work of the experimental breeders such as Kölreuter, Knight, Herbert, Gärtner, Wichura, Godron, Naudin, and many more. To have treated as non-existent the work of this group of naturalists, who alone have attempted to solve the problems

* *Grammar of Science*, 2nd ed. 1900, p. 480.

† *Phil. Trans.* 1900, vol. 195, A, p. 121.

of heredity and species—Evolution, as we should now say—by the only sound method—*experimental breeding*—to leave out of consideration almost the whole block of evidence collected in *Animals and Plants*—Darwin's finest legacy as I venture to declare—was unfortunate on the part of any exponent of Heredity, and in the writings of a professed naturalist would have been unpardonable. But even as modified in 1900 the Law of Ancestral Heredity is heavily over-sparred, and any experimental breeder could have increased Pearson's list of unconformable cases by as many again.

But to return to Professor Weldon. He now repeats that the Law of Ancestral Heredity seems likely to prove generally applicable to *blended* inheritance, but that the case of *alternative* inheritance is for the present reserved. We should feel more confidence in Professor Weldon's exposition if he had here reminded us that the special case which fitted Galton's Law so well that it emboldened him to announce that principle as apparently "universally applicable to bi-sexual descent" was one of *alternative* inheritance—namely the coat-colour of Basset-hounds. Such a fact is, to say the least, ominous. Pearson, in speaking (1900) of this famous case of Galton's, says that these phenomena of alternative inheritance must be treated separately (from those of blended inheritance)*, and for them he deduces a proposed "*law of reversion*," based of course on ancestry. He writes, "In both cases we may speak of a law of ancestral heredity, but the first predicts the probable character of the individual produced by a

* "If this be done, we shall, I venture to think, keep not only our minds, but our points for observation, clearer; and further, the failure of Mr Galton's statement in the one case will not in the least affect its validity in the other." Pearson (32), p. 143.

given ancestry, while the second tells us the percentages of the total offspring which on the average revert to each ancestral type*."

With the distinctions between the original Law of Ancestral Heredity, the modified form of the same law, and the Law of Reversion, important as all these considerations are, we are not at present concerned.

For the Mendelian principle of heredity asserts a proposition absolutely at variance with all the laws of ancestral heredity, however formulated. In those cases to which it applies strictly, this principle declares that the cross-breeding of parents *need* not diminish the purity of their germ-cells or consequently the purity of their offspring. When in such cases individuals bearing opposite characters, A and B, are crossed, the germ-cells of the resulting cross-bred, AB, are each to be bearers either of character A or of character B, not both.

Consequently when the cross-breds breed either together or with the pure forms, individuals will result of the forms AA, AB, BA, BB†. Of these the forms AA and BB, formed by the union of similar germs, are stated to be as pure as if they had had no cross in their pedigree, and henceforth their offspring will be no more likely to depart from the A type or the B type respectively, than those of any other originally pure specimens of these types.

Consequently in such examples it is *not* the fact that each ancestor must be brought to account as the Galton-Pearson Law asserts, and we are clearly dealing with a physiological phenomenon not contemplated by that Law at all.

* *Grammar of Science*, 1900, p. 494. See also Pearson, *Proc. Roy. Soc.* 1900, LXVI. pp. 142-3.

† On an average of cases, in equal numbers, as Mendel found.

Every case therefore which obeys the Mendelian principle is in direct contradiction to the proposition to which Professor Weldon's school is committed, and it is natural that he should be disposed to consider the Mendelian principle as applying especially to "alternative" inheritance, while the law of Galton and Pearson is to include the phenomenon of blended inheritance. The latter, he tells us, is "the most usual case," a view which, if supported by evidence, might not be without value.

It is difficult to blame those who on first acquaintance concluded Mendel's principle can have no strict application save to alternative inheritance. Whatever blame there is in this I share with Professor Weldon and those whom he follows. Mendel's own cases were almost all alternative; also the fact of dominance is very dazzling at first. But that was two years ago, and when one begins to see clearly again, it does not look so certain that the real essence of Mendel's discovery, the purity of germ-cells in respect of certain characters, may not apply also to some phenomena of blended inheritance. The analysis of this possibility would take us to too great length, but I commend to those who are more familiar with statistical method, the consideration of this question: whether dominance being absent, indefinite, or suppressed, the phenomena of heritages completely blended in the zygote, may not be produced by gametes presenting Mendelian purity of characters. A brief discussion of this possibility is given in the Introduction, p. 31.

Very careful inquiry would be needed before such a possibility could be negatived. For example, we know that the Laws based on Ancestry can apply to *alternative* inheritance; witness the case of the Basset-hounds. Here there is no simple Mendelian dominance; but are we sure

there is no purity of germ-cells? The new conception goes a long way and it may well reach to such facts as these.

But for the present we will assume that Mendel's principle applies only to *certain phenomena of alternative inheritance*, which is as far as our warrant yet runs.

No close student of the recent history of evolutionary thought needs to be told what the attitude of Professor Weldon and his followers has been towards these same disquieting .and unwelcome phenomena of alternative inheritance and discontinuity in variation. Holding at first each such fact for suspect, then treating them as rare and negligible occurrences, he and his followers have of late come slowly to accede to the facts of discontinuity a bare and grudging recognition in their scheme of evolution*.

Therefore on the announcement of that discovery which once and for all ratifies and consolidates the conception of discontinuous variation, and goes far to define that of alternative inheritance, giving a finite body to what before was vague and tentative, it is small wonder if Professor Weldon is disposed to criticism rather than to cordiality.

We have now seen what is the essence of Mendel's discovery based on a series of experiments of unequalled simplicity which Professor Weldon does not venture to dispute.

* Read in this connexion Pearson, K., *Grammar of Science*, 2nd ed. 1900, pp. 390—2.

Professor Weldon even now opens his essay with the statement—or perhaps reminiscence—that "it is perfectly possible and indeed probable that the difference between these forms of inheritance [blended, mosaic, and alternative] is only one of degree." This may be true; but reasoning favourable to this proposition could equally be used to prove the difference between mechanical mixture and chemical combination to be a difference of degree.

II. Mendel and the Critic's Version of him.

The "Law of Dominance."

I proceed to the question of dominance which Professor Weldon treats as a prime issue, almost to the virtual concealment of the great fact of gametic purity.

Cross-breds in general, AB and BA, named above, may present many appearances. They may all be indistinguishable from A, or from B; some may appear A's and some B's; they may be patchworks of both; they may be blends presenting one or many grades between the two; and lastly they *may have an appearance special to themselves* (*being in the latter case, as it often happens, "reversionary"*), a possibility which Professor Weldon does not stop to consider, though it is the clue that may unravel many of the facts which mystify him now.

Mendel's discovery became possible because he worked with regular cases of the first category, in which he was able to recognize that *one* of each of the pairs of characters he studied *did* thus prevail and *was* "dominant" in the cross-bred to the exclusion of the other character. This fact, which is still an accident of particular cases, Professor Weldon, following some of Mendel's interpreters, dignifies by the name of the "Law of Dominance," though he omits to warn his reader that Mendel states no "Law of Dominance" whatever. The whole question whether one or other character of the antagonistic pair is dominant though of great importance is logically a subordinate one. It depends on the specific nature of the varieties and individuals used, sometimes probably on the influence of

external conditions and on other factors we cannot now discuss. There is as yet no universal law here perceived or declared.

Professor Weldon passes over the proof of the purity of the germ-cells lightly enough, but this proposition of dominance, suspecting its weakness, he puts prominently forward. Briefest equipment will suffice. Facing, as he supposes, some new pretender—some local Theudas—offering the last crazy prophecy,—any argument will do for such an one. An eager gathering in an unfamiliar literature, a scrutiny of samples, and he will prove to us with small difficulty that dominance of yellow over green, and round over wrinkled, is irregular even in peas after all; that in the sharpness of the discontinuity exhibited by the variations of peas there are many grades; that many of these grades co-exist in the same variety; that some varieties may perhaps be normally intermediate. All these propositions are supported by the production of a collection of evidence, the quality of which we shall hereafter consider. "Enough has been said," he writes (p. 240), "to show the grave discrepancy between the evidence afforded by Mendel's own experiments and that obtained by other observers, equally competent and trustworthy."

We are asked to believe that Professor Weldon has thus discovered "a fundamental mistake" vitiating all that work, the importance of which, he elsewhere tells us, he has "no wish to belittle."

III. The Facts in regard to Dominance of Characters in Peas.

Professor Weldon refers to no experiments of his own and presumably has made none. Had he done so he would have learnt many things about dominance in peas, whether of the yellow cotyledon-colour or of the round form, that might have pointed him to caution.

In the year 1900 Messrs Vilmorin-Andrieux & Co. were kind enough to send to the Cambridge Botanic Garden on my behalf a set of samples of the varieties of *Pisum* and *Phaseolus*, an exhibit of which had greatly interested me at the Paris Exhibition of that year. In the past summer I grew a number of these and made some preliminary cross-fertilizations among them (about 80 being available for these deductions) with a view to a future study of certain problems, Mendelian and others. In this work I had the benefit of the assistance of Miss Killby of Newnham College. Her cultivations and crosses were made independently of my own, but our results are almost identical. The experience showed me, what a naturalist would expect and practical men know already, that *a great deal turns on the variety used*; that some varieties are very sensitive to conditions while others maintain their type sturdily; that in using certain varieties Mendel's experience as to dominance is regularly fulfilled, while in the case of other varieties irregularities and even some contradictions occur. That the dominance of yellow cotyledon-colour over green, and the dominance of the smooth form over the wrinkled, is a *general* truth for *Pisum sativum* appears at once; that it is a universal truth I cannot believe any competent naturalist would imagine, still less assert. Mendel certainly never did.

When he speaks of the "law" or "laws" that he has established for *Pisum* he is referring to his own discovery of the purity of the germ-cells, that of the statistical distribution of characters among them, and the statistical grouping of the different germ-cells in fertilization, and not to the "Law of Dominance" which he never drafted and does not propound.

The issue will be clearer if I here state briefly what, as far as my experience goes, are the facts in regard to the characters *cotyledon-colour* and *seed-shapes* in peas. I have not opportunity for more than a passing consideration of the *seed-coats* of pure forms*; that is a maternal character, a fact I am not sure Professor Weldon fully appreciates. Though that may be incredible, it is evident from many passages that he has not, in quoting authorities, considered the consequences of this circumstance.

The normal characters: colour of cotyledons and seed-coats.

Culinary peas (*P. sativum*, omitting purple sorts) can primarily be classified on colour into two groups, yellow and green. In the green certain pigmentary matters persist in the ripe seed which disappear or are decomposed in the yellow as the seed ripens. But it may be observed

* The whole question as to seed-coat colour is most complex. Conditions of growth and ripening have a great effect on it. Mr Arthur Sutton has shown me samples of *Ne Plus Ultra* grown in England and abroad. This pea has yellow cotyledons with seed-coats either yellow or "blue." The foreign sample contained a much greater proportion of the former. He told me that generally speaking this is the case with samples ripened in a hot, dry climate.

Unquestionable Xenia appears occasionally, and will be spoken of later. Moreover to experiment with such a *plant*-character an extra generation has to be sown and cultivated. Consequently the evidence is meagre.

that the "green" class itself is treated as of two divisions, *green* and *blue*. In the seedsmen's lists the classification is made on the *external appearance* of the seed, without regard to whether the colour is due to the seed-coat, the cotyledons, or both. As a rule perhaps yellow coats contain yellow cotyledons, and green coats green cotyledons, though yellow cotyledons in green coats are common, e.g. *Gradus*, of which the cotyledons are yellow while the seed-coats are about as often green as yellow (or "white," as it is called technically). Those called "blue" consist mostly of seeds which have green cotyledons seen through transparent skins, or yellow cotyledons combined with green skins. The skins may be roughly classified into thin and transparent, or thick and generally at some stage pigmented. In numerous varieties the colour of the cotyledon is wholly yellow, or wholly green. Next there are many varieties which are constant in habit and other properties but have seeds belonging to these two colour categories in various proportions. How far these proportions are known to be constant I cannot ascertain.

Of such varieties showing mixture of *cotyledon*-colours nearly all can be described as dimorphic in colour. For example in Sutton's *Nonpareil Marrowfat* the cotyledons are almost always *either* yellow *or* green, with some piebalds, and the colours of the seed-coats are scarcely less distinctly dimorphic. In some varieties which exist in both colours intermediates are so common that one cannot assert any regular dimorphism*.

* Knowing my interest in this subject Professor Weldon was so good as to forward to me a series of his peas arranged to form a scale of colours and shapes, as represented in his Plate I. I have no doubt that the use of such colour-scales will much facilitate future study of these problems.

There are some varieties which have cotyledons green and intermediate shading to greenish yellow, like *Stratagem* quoted by Professor Weldon. Others have yellow and intermediate shading to yellowish green, such as McLean's *Best of all**. I am quite disposed to think there may be truly monomorphic varieties with cotyledons permanently of intermediate colour only, but so far I have not seen one†. The variety with greatest *irregularity* (apart from regular dimorphism) in cotyledon-colour I have seen is a sample of "*mange-tout à rames, à grain vert,*" but it was a good deal injured by weevils (*Bruchus*), which always cause irregularity or change of colour.

Lastly in some varieties there are many piebalds or mosaics.

From what has been said it will be evident that the description of a pea in an old book as having been green, blue, white, and so forth, unless the cotyledon-colour is distinguished from seed-coat colour, needs careful consideration before inferences are drawn from it.

Shape.

In regard to shape, if we keep to ordinary shelling peas, the facts are somewhat similar, but as shape is probably more sensitive to conditions than cotyledon-colour (not than *seed-coat* colour) there are irregularities to be perhaps ascribed to this cause. Broadly, however, there are two main divisions, round and wrinkled. It is unquestioned that between these two types every intermediate occurs.

* I notice that Vilmorin in the well-known *Plantes Potagères*, 1883, classifies the intermediate-coloured peas with the *green*.

† Similarly though *tall* and *dwarf* are Mendelian characters, peas occur of all heights and are usually classified as tall, half-dwarfs, and dwarfs.

Here again a vast number of varieties can be at once classified into round and wrinkled (the classification commonly used), others are intermediate normally. Here also I suspect some fairly clear sub-divisions might be made in the wrinkled group and in the round group too, but I would not assert this as a fact.

I cannot ascertain from botanists what is the nature of the difference between round and wrinkled peas, though no doubt it will be easily discovered. In maize the round seeds contain much unconverted starch, while in the wrinkled or sugar-maize this seems to be converted in great measure as the seed ripens; with the result that, on drying, the walls collapse. In such seeds we may perhaps suppose that the process of conversion, which in round seeds takes place on germination, is begun earlier, and perhaps the variation essentially consists in the premature appearance of the converting ferment. It would be most rash to suggest that such a process may be operating in the pea, for the phenomenon may have many causes; but however that may be, there is evidently a difference of such a nature that when the water dries out of the seed on ripening, its walls collapse*; and this collapse may occur in varying degrees.

* Wrinkling must of course be distinguished further from the squaring due to the peas pressing against each other in the pod.

In connexion with these considerations I may mention that Vilmorin makes the interesting statement that most peas retain their vitality three years, dying as a rule rapidly after that time is passed, though occasionally seeds seven or eight years old are alive; but that *wrinkled* peas germinate as a rule less well than round, and do not retain their vitality so long as the round. Vilmorin-Andrieux, *Plantes Potagères*, 1883, p. 423. Similar statements regarding the behaviour of wrinkled peas in India are made by Firminger, *Gardening for India*, 3rd ed. 1874, p. 146.

In respect of *shape* the seeds of a variety otherwise stable are as a rule fairly uniform, the co-existence of both shapes and of intermediates between them in the same variety is not infrequent. As Professor Weldon has said, *Telephone* is a good example of an extreme case of mixture of both colours and shapes. *William I.* is another. It may be mentioned that regular dimorphism in respect of shape is not so common as dimorphism in respect of colour. Of great numbers of varieties seen at Messrs Suttons' I saw none so distinctly dimorphic in shape as *William I.* which nevertheless contains all grades commonly.

So far I have spoken of the shapes of ordinary English culinary peas. But if we extend our observations to the shapes of *large-seeded* peas, which occur for the most part among the sugar-peas (*mange-touts*), of the "grey" peas with coloured flowers, etc., there are fresh complications to be considered.

Professor Weldon does not wholly avoid these (as Mendel did in regard to shape) and we will follow him through his difficulties hereafter. For the present let me say that the classes *round* and *wrinkled* are not readily applicable to those other varieties and are not so applied either by Mendel or other practical writers on these subjects. To use the terms indicated in the Introduction, *seed-shape* depends on more than one pair of allelomorphs—possibly on several.

Stability and Variability.

Generally speaking peas which when seen in bulk are monomorphic in colour and shape, will give fairly true and uniform offspring (but such strict monomorphism is rather exceptional). Instances to the contrary occur, and in my own brief experience I have seen some. In a row of *Fill-*

basket grown from selected seed there were two plants of different habit, seed-shape, etc. Each bore pods with seeds few though large and round. Again *Blue Peter* (blue and round) and *Laxton's Alpha* (blue and wrinkled), grown in my garden and left to nature uncovered, have each given a considerable proportion of seeds with *yellow* cotyledons, about 20 % in the case of *Laxton's Alpha*. The distribution of these on the plants I cannot state. The plants bearing them in each case sprang from green-cotyledoned seeds taken from samples containing presumably unselected green seeds only. A part of this exceptional result may be due to crossing, but heterogeneity of conditions* especially in or after ripening is a more likely cause, hypotheses I hope to investigate next season. Hitherto I had supposed the crossing, if any, to be done by *Bruchus* or Thrips, but Tschermak also suspects *Megachile*, the leaf-cutter bee, which abounds in my garden.

Whatever the cause, these irregularities may undoubtedly occur; and if they be proved to be largely independent of crossing and conditions, this will in nowise vitiate the truth of the Mendelian principle. For in that case it may simply be variability. Such true variation, or sporting, in the pea is referred to by many observers. Upon this subject I have received most valuable facts from Mr Arthur Sutton, who has very kindly interested himself in these inquiries.

* Cotyledon-colour is not nearly so sensitive to ordinary changes in conditions as coat-colour, provided the coat be uninjured. But even in monomorphic *green* varieties, a seed which for any cause has burst on ripening, has the exposed parts of its cotyledons *yellow*. The same may be the case in seeds of green varieties injured by *Bruchus* or birds. These facts make one hesitate before denying the *effects of conditions on the cotyledon-colour* even of uninjured seeds, and the variation described above may have been simply weathering. The seeds were gathered very late and many were burst in *Laxton's Alpha*. I do not yet know they are alive.

He tells me that several highly bred varieties, selected with every possible care, commonly throw a small but constant proportion of poor and almost vetch-like plants, with short pods and small round seeds, which are hoed out by experienced men each year before ripening. Other high-class varieties always, wherever grown, and when far from other sorts, produce a small percentage of some one or more definite "sports." Of these peculiar sports he has sent me a collection of twelve, taken from as many standard varieties, each "sport" being represented by eight seeds, which though quite distinct from the type agree with each other in almost all cases.

In two cases, he tells me, these seed-sports sown separately have been found to give plants identical with the standard type and must therefore be regarded as sports in *seed characters* only; in other cases change of plant-type is associated with the change of seed-type.

In most standard varieties these definite sports are not very common, but in a few they are common enough to require continual removal by selection*.

I hope before long to be able to give statistical details

* It is interesting to see that in at least one case the same—or practically the same—variety has been independently produced by different raisers, as we now perceive, by the fortuitous combination of similar allelomorphs. *Sutton's Ringleader* and *Carter's First Crop* (and two others) are cases in point, and it is peculiarly instructive to see that in the discussion of these varieties when they were new, one of the points indicating their identity was taken to be the fact that they produced *the same "rogues."* See *Gard. Chron.* 1865, pp. 482 and 603; 1866, p. 221; 1867, pp. 546 and 712.

Rimpau quotes Blomeyer (*Kultur der Landw. Nutzpflanzen*, Leipzig, 1889, pp. 357 and 380) to the effect that *purple*-flowered plants with *wrinkled* seeds may spring as direct sports from peas with *white* flowers and *round* seeds. I have not seen a copy of Blomeyer's work. Probably this "wrinkling" was "indentation."

and experiments relating to this extraordinarily interesting subject. As de Vries writes in his fine work *Die Mutationstheorie* (I. p. 580), "a study of the seed-differences of inconstant, or as they are called, '*still*' unfixed varieties, is a perfect treasure-house of new discoveries."

Let us consider briefly the possible significance of these facts in the light of Mendelian teaching. First, then, it is clear that as regards most of such cases the hypothesis is not excluded that these recurring sports may be due to the fortuitous concurrence of certain scarcer hypallelomorphs, which may either have been free in the original parent varieties from which the modern standard forms were raised, or may have been freed in the crossing to which the latter owe their origin (see p. 28). This possibility raises the question whether, if we could make "*pure* cultures" of the gametes, any variations of this nature would ever occur. This may be regarded as an unwarrantable speculation, but it is not wholly unamenable to the test of experiments.

But variability, in the sense of division of gonads into heterogeneous gametes, may surely be due to causes other than crossing. This we cannot doubt. Cross-fertilization of the zygote producing those gametes is *one* of the causes of such heterogeneity among them. We cannot suppose it to be the sole cause of this phenomenon.

When Mendel asserts the purity of the germ-cells of cross-breds he cannot be understood to mean that they are *more pure* than those of the original parental races. These must have varied in the past. The wrinkled seed arose from the round, the green from the yellow (or *vice versâ*, if preferred), and probably numerous intermediate forms from both.

The variations, or as I provisionally conceive it, that differentiant division among the gametes of which variation

(neglecting environment) is the visible expression, has arisen and can arise at one or more points of time, and we have no difficulty in believing it to occur now. In many cases we have clear evidence that it does. Crossing,—dare we call it asymmetrical fertilization?—is *one* of the causes of the production of heterogeneous gametes—the result of divisions qualitatively differentiant and perhaps asymmetrical*.

There are other causes and we have to find them. Some years ago I wrote that consideration of the causes of variation was in my judgment premature†. Now that through Mendel's work we are clearing our minds as to the fundamental nature of "gametic" variation, the time is approaching when an investigation of such causes may be not unfruitful.

Of *variation* as distinct from *transmission* why does Professor Weldon take no heed? He writes (p. 244):

> "If Mendel's statements were universally valid, even among Peas, the characters of the seeds in the numerous hybrid races now existing should fall into one or other of a few definite categories, which should not be connected by intermediate forms."

Now, as I have already pointed out, Mendel made no pretence of universal statement: but had he done so, the conclusion, which Professor Weldon here suggests should follow from such a universal statement, is incorrectly drawn. Mendel is concerned with the laws of *transmission*

* The asymmetries here conceived may of course be combined in an inclusive symmetry. Till the differentiation can be optically recognized in the gametes we shall probably get no further with this part of the problem.

† *Materials for the Study of Variation*, 1894, p. 78.

of existing characters, not with *variation*, which he does not discuss.

Nevertheless Professor Weldon has some acquaintance with the general fact of variability in certain peas, which he mentions (p. 236), but the bearing of this fact on the difficulty he enuntiates escapes him.

Results of crossing in regard to seed characters: normal and exceptional.

The conditions being the same, the question of the characters of the cross-bred zygotes which we will call AB's depends primarily on the specific nature of the varieties which are crossed to produce them. It is unnecessary to point out that if all AB's are to look alike, both the varieties A and B must be *pure*—not in the common sense of descended, as far as can be traced, through individuals identical with themselves, but pure in the Mendelian sense, that is to say that each must be at that moment producing only homogeneous gametes bearing the same characters A and B respectively. Purity of pedigree in the breeder's sense is a distinct matter altogether. The length of time—or if preferred—the number of generations through which a character of a variety has remained pure, alters the probability of its *dominance*, i.e. its appearance when a gamete bearing it meets another bearing an antagonistic character, no more, so far as we are yet aware, than the length of time a stable element has been isolated alters the properties of the chemical compound which may be prepared from it.

Now when individuals (bearing contrary characters), pure in the sense indicated, are crossed together, the question arises, What will be the appearance of the first

cross individuals? Here again, *generally speaking*, when thoroughly green cotyledons are crossed with thoroughly yellow cotyledons, the first-cross seeds will have yellow cotyledons; when fully round peas are crossed with fully wrinkled the first result will *generally speaking* be *round*, often with slight pitting as Mendel has stated. This has been the usual experience of Correns, Tschermak, Mendel, and myself* and, as we shall see, the amount of clear and substantial evidence to the contrary is still exceedingly small. But as any experienced naturalist would venture to predict, there is no *universal* rule in the matter. As Professor Weldon himself declares, had there been such a universal rule it would surely have been notorious. He might further have reflected that in Mendel's day, when hybridisation was not the *terra incognita* it has since become, the assertion of such universal propositions would have been peculiarly foolish. Mendel does not make it; but Professor Weldon perceiving the inherent improbability of the assertion conceives at once that Mendel *must* have made it, and if Mendel doesn't say so in words then he must have implied it. As a matter of fact Mendel never treats dominance as more than an incident in his results, merely using it as a means to an end, and I see no reason to suppose he troubled to consider to what extent the phenomenon is or is not universal—a matter with which he had no concern.

* The varieties used were *Express*, *Laxton's Alpha*, *Fillbasket*, *McLean's Blue Peter*, *Serpette nain blanc*, *British Queen*, *très nain de Bretagne*, Sabre, *mange-tout* Debarbieux, and a large "grey" sugar-pea, *pois sans parchemin géant à très large cosse*. Not counting the last two, five are round and three are wrinkled. As to cotyledons, six have yellow and four have green. In about 80 crosses I saw no exception to dominance of yellow; but one apparently clear case of dominance of wrinkled and some doubtful ones.

Of course there may be exceptions. As yet we cannot detect the causes which control them, though injury, impurity, accidental crossing, mistakes of various kinds, account for many. Mendel himself says, for instance, that unhealthy or badly grown plants give uncertain results. Nevertheless there seems to be a true residuum of exceptions not to be explained away. I will recite some that I have seen. In my own crosses I have seen green × green give yellow four times. This I incline to attribute to conditions or other disturbance, for the natural pods of these plants gave several yellows. At Messrs Suttons' I saw second-generation seeds got by allowing a cross of *Sutton's Centenary* (gr. wr.) × *Eclipse* (gr. rd.) to go to seed; the resulting seeds were both green and *yellow*, wrinkled and round. But in looking at a sample of *Eclipse* I found a few *yellow* seeds, say two per cent., which may perhaps be the explanation. Green wrinkled × green round *may* give all wrinkled, and again wrinkled × wrinkled may give *round**. Of this I saw a clear case—supposing no mistake to have occurred—at Messrs Suttons'. Lastly we have the fact that in exceptional cases crossing two forms—apparently pure in the strict sense—may give a mixture in the *first* generation. There are doubtless examples also of unlikeness between reciprocals, and of this too I have seen one putative case†.

Such facts thus set out for the first cross-bred generation may without doubt be predicated for subsequent generations.

What then is the significance of the facts?

* Professor Weldon may take this as a famous blow for Mendel, till he realizes what is meant by Mendel's "Hybrid-character."

† In addition to those spoken of later, where the great difference between reciprocals is due to the *maternal* characters of the seeds.