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 fundamentally 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 consider-tion 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.

Analysis of exceptions.

Assuming that all these "contradictory" phenomena happened truly as alleged, and were not pathological or due to error—an explanation which seems quite inadequate—there are at least four possible accounts of such diverse results—each valid, without any appeal to ancestry.

1. That dominance may exceptionally fail—or in other words be created on the side which is elsewhere recessive. For this exceptional failure we have to seek exceptional causes. The artificial *creation* of dominance (in a character usually recessive) has not yet to my knowledge been demonstrated experimentally, but experiments are begun by which such evidence may conceivably be obtained.

2. There may be what is known to practical students of evolution as the *false hybridism of Millardet*, or in other words, fertilisation with—from unknown causes—transmission of none or of only some of the characters of one pure parent. The applicability of this hypothesis to the colours and shapes of peas is perhaps remote, but we may notice that it is one possible account of those rare cases where two pure forms give a *mixed* result in the first generation, even assuming the gametes of each pure parent to be truly monomorphic as regards the character they bear. The applicability of this suggestion can of course be tested by study of the subsequent generations, self-fertilised or fertilised by similar forms produced in the same way. In the case of a *genuine* false-hybrid the lost characters will not reappear in the posterity.

3. The result may not be a case of transmission at all as it is at present conceived, but of the creation on crossing

of something *new*. Our *AB*'s may have one or more characters *peculiar to themselves*. We may in fact have made a distinct "mule" or heterozygote form. Where this is the case, there are several subordinate possibilities we need not at present pursue.

4. There may be definite *variation* (distinct from that proper to the "mule") consequent on causes we cannot yet surmise (see pp. 125 and 128).

The above possibilities are I believe at the present time the only ones that need to be considered in connexion with these exceptional cases*. They are all of them capable of experimental test and in certain instances we are beginning to expect the conclusion.

The "mule" or heterozygote.

There can be little doubt that in many cases it is to the third category that the phenomena belong. An indication of the applicability of this reasoning will generally be found in the fact that in such "mule" forms the colour or the shape of the seeds will be recognizably peculiar and proper to the specimens themselves, as distinct from their parents, and we may safely anticipate that when those seeds are grown the plants will show some character which is recognizable as novel. The *proof* that the reasoning may apply can as yet only be got by finding that the forms in

* I have not here considered the case in which male and female elements of a pure variety are not homologous and the variety is a *permanent* monomorphic "mule." Such a phenomenon, when present, will prove itself in reciprocal crossing. I know no such case in peas for certain.

question cannot breed true even after successive selections, but constantly break up into the same series of forms*.

This conception of the "mule" form, or "hybrid-character" as Mendel called it, though undeveloped, is perfectly clear in his work. He says that the dominant character may have two significations, it may be *either* a parental character or a hybrid-character, and it must be differentiated according as it appears in the one capacity or the other. He does not regard the character displayed by the hybrid, whether dominant or other, *as a thing inherited from or transmitted by the pure parent at all, but as the peculiar function or property of the hybrid.* When this conception has been fully understood and appreciated in all its bearings it will be found to be hardly less fruitful than that of the purity of the germ-cells.

The two parents are two—let us say—substances† represented by corresponding gametes. These gametes unite to form a new "substance"—the cross-bred zygote. This has its own properties and structure, just as a chemical compound has, and the properties of this new "substance" are *not more strictly* traceable to, or "inherited" from, those of the two parents than are those of a new chemical compound "inherited" from those of the component elements. If the case be one in which the gametes are pure, the new "substance" is not represented by them, but the compound is again dissociated into its components, each of which is separately represented by gametes.

* It will be understood that a "mule" form is quite distinct from what is generally described as a "blend." One certain criterion of the "mule" form is the fact that it cannot be fixed, see p. 25. There is little doubt that Laxton had such a "mule" form when he speaks of "the remarkably fine but unfixable pea, Evolution." *J. R. Hort. Soc.* XII. 1890, p. 37 (*v. infra*).

† Using the word metaphorically.

The character of the cross-bred zygote may be anything. It may be something we have seen before in one or other of the parents, it may be intermediate between the two, or it may be something new. All these possibilities were known to Mendel and he is perfectly aware that his principle is equally applicable to all. The first case is his "dominance." That he is ready for the second is sufficiently shown by his brief reference to time of flowering considered as a character (p. 65). The hybrids, he says, flower at a time *almost exactly intermediate* between the flowering times of the parents, and he remarks that the development of the hybrids in this case probably happens in the same way as it does in the case of the other characters*.

That he was thoroughly prepared for the third possibility appears constantly through the paper, notably in the argument based on the *Phaseolus* hybrids, and in the statement that the hybrid between talls and dwarfs is generally taller than the tall parent, having increased height as its "hybrid-character."

All this Professor Weldon has missed. In place of it he offers us the *sententia* that no one can expect to understand these phenomena if he neglect ancestry. This is the idle gloss of the scribe, which, if we erase it not thoroughly, may pass into the text.

Enough has been said to show how greatly Mendel's conception of heredity was in advance of those which pass current at the present day; I have here attempted

* "*Ueber die Blüthezeit der Hybriden sind die Versuche noch nicht abgeschlossen. So viel kann indessen schon angegeben werden, dass dieselbe fast genau in der Mitte zwischen jener der Samen- und Pollenpflanze steht, und die Entwicklung der Hybriden bezüglich dieses Merkmales wahrscheinlich in der nämlichen Weise erfolgt, wie es für die übrigen Merkmale der Fall ist.*" Mendel, p. 23.

the barest outline of the nature of the "hybrid-character," and I have not sought to indicate the conclusions that we reach when the reasoning so clear in the case of the hybrid is applied to the pure forms and their own characters.

In these considerations we reach the very base on which all conceptions of heredity and variation must henceforth rest, and that it is now possible for us to attempt any such analysis is one of the most far-reaching consequences of Mendel's principle. Till two years ago no one had made more than random soundings of this abyss.

I have briefly discussed these possibilities to assist the reader in getting an insight into Mendel's conceptions. But in dealing with Professor Weldon we need not make this excursion ; for his objection arising from the absence of uniform regularity in dominance is not in point.

The soundness of Mendel's work and conclusions would be just as complete if dominance be found to fail often instead of rarely. For it is perfectly certain that varieties *can* be chosen in such a way that the dominance of one character over its antagonist is so regular a phenomenon that it *can* be used in the way Mendel indicates. He chose varieties, in fact, in which a known character *was* regularly dominant and it is because he did so that he made his discovery*. When Professor Weldon speaks of the existence of fluctuation and diversity in regard to dominance as proof of a "grave discrepancy" between Mendel's facts and those of other observers†, he merely indicates the point at which his own misconceptions began.

* As has been already shown the discovery could have been made equally well and possibly with greater rapidity in a case in which the hybrid had a character distinct from either parent. The cases that would *not* have given a clear result are those where there is irregular dominance of one or other parent.

† Weldon, p. 240.

From Mendel's style it may be inferred that if he had meant to state universal dominance in peas he would have done so in unequivocal language. Let me point out further that of the 34 varieties he collected for study, he discarded 12 as not amenable to his purposes*. He tells us he would have nothing to do with characters which were not sharp, but of a "more or less" description. As the 34 varieties are said to have all come true from seed, we may fairly suppose that the reason he discarded twelve was that they were unsuitable for his calculations, having either ill-defined and intermediate characters, or possibly defective and irregular dominance.

IV. PROFESSOR WELDON'S COLLECTION OF "OTHER EVIDENCE CONCERNING DOMINANCE IN PEAS."

A. In regard to cotyledon colour: Preliminary.

I have been at some pains to show how the contradictory results, no doubt sometimes occurring, on which Professor Weldon lays such stress, may be comprehended without any injury to Mendel's main conclusions. This excursion was made to save trouble with future discoverers of exceptions, though the existence of such facts need scarcely disturb many minds. As regards the dominance of yellow cotyledon-colour over green the whole number of genuine unconformable cases is likely to prove very small indeed, though in regard to the dominance of round shape over wrinkled we may be prepared for more discrepancies. Indeed my own crosses alone are sufficient to show that in using some varieties irregularities are to be expected.

* See p. 43.

Considering also that the shapes of peas depend unquestionably on more than one pair of allelomorphs I fully expect regular blending in some cases.

As however it may be more satisfactory to the reader and to Professor Weldon if I follow him through his "contradictory" evidence I will endeavour to do so. Those who have even a slight practical acquaintance with the phenomena of heredity will sympathize with me in the difficulty I feel in treating this section of his arguments with that gravity he conceives the occasion to demand.

In following the path of the critic it will be necessary for me to trouble the reader with a number of details of a humble order, but the journey will not prove devoid of entertainment.

Now exceptions are always interesting and suggestive things, and sometimes hold a key to great mysteries. Still when a few exceptions are found disobeying rules elsewhere conformed to by large classes of phenomena it is not an unsafe course to consider, with such care as the case permits, whether the exceptions may not be due to exceptional causes, or failing such causes whether there may be any possibility of error. But to Professor Weldon, an exception is an exception—and as such may prove a very serviceable missile; so he gathers them as they were "smooth stones from the brook."

Before examining the quality of this rather miscellaneous ammunition I would wish to draw the non-botanical reader's attention to one or two facts of a general nature.

For our present purpose the seed of a pea may be considered as consisting of two parts, the *embryo with its cotyledons*, enclosed in a *seed-coat*. It has been known for about a century that this coat or skin is a *maternal* structure, being part of the mother plant just as much as the pods are, and consequently not belonging to the next generation at all. If then any changes take place in it consequent on fertilisation, they are to be regarded not as in any sense a transmission of character by heredity, but rather as of the nature of an "infection." If on the other hand it is desired to study the influence of hereditary transmission on seed-coat characters, then the crossed seeds must be sown and the seed-coats of their seeds studied. Such infective changes in maternal tissues have been known from early times, a notable collection of them having been made especially by Darwin; and for these cases Focke suggested the convenient word *Xenia*. With this familiar fact I would not for a moment suppose Professor Weldon unacquainted, though it was with some surprise that I found in his paper no reference to the phenomenon.

For as it happens, xenia is not at all a rare occurrence with *certain varieties* of peas; though in them, as I believe is generally the case with this phenomenon, it is highly irregular in its manifestations, being doubtless dependent on slight differences of conditions during ripening.

The coats of peas differ greatly in different varieties, being sometimes thick and white or yellow, sometimes thick and highly pigmented with green or other colours, in both of which cases it may be impossible to judge the cotyledon-colour without peeling off the opaque coat; or the coats may be very thin, colourless and transparent, so that the cotyledon-colour is seen at once. It was such a transparent form that Mendel says he used for his experiments with cotyledon-colour. In order to see xenia a pea with a *pigmented* seed-coat should be taken as seed-parent, and crossed with a variety having a different cotyledon-colour. There is then a fair chance of seeing this phenomenon, but much still depends on the variety. For example, *Fillbasket* has green cotyledons and seed-coat green except near the hilar surface. Crossed with *Serpette nain blanc* (yellow cotyledons and yellow coat) this variety gave three pods with 17 seeds in which the seed-coats were almost full yellow (xenia). Three other pods (25 seeds), similarly produced, showed slight xenia, and one pod with eight seeds showed little or none.

On the other hand *Fillbasket* fertilised with *nain de Bretagne* (yellow cotyledons, seed-coats yellow to yellowish green) gave six pods with 39 seeds showing slight xenia, distinct in a few seeds but absent in most.

Examples of xenia produced by the contrary proceeding, namely fertilising a yellow pea with a green, may indubitably occur and I have seen doubtful cases; but as by the nature of the case these are *negative* phenomena, i.e. the seed-coat remaining greenish and *not* going through its normal maturation changes, they must always be equivocal, and would require special confirmation before other causes were excluded.

Lastly, the special change (xenia) Mendel saw in "grey" peas, appearance or increase of purple pigment in the thick coats, following crossing, is common but also irregular.

If a *transparent* coated form be taken as seed-parent there is no appreciable xenia, so far as I know, and such a phenomenon would certainly be paradoxical*.

In this connection it is interesting to observe that Giltay, whom Professor Weldon quotes as having obtained purely Mendelian results, got no xenia though searching for it. If the reader goes carefully through Giltay's numerous cases, he will find, *almost* without doubt, that none of them were such as produce it. *Reading Giant*, as

* In some transparent coats there is pigment, but so little as a rule that xenia would be scarcely noticeable.

Giltay states, has a *transparent* skin, and the only xenia likely to occur in the other cases would be of the peculiar and uncertain kind seen in using "grey" peas. Professor Weldon notes that Giltay, who evidently worked with extreme care, *peeled* his seeds before describing them, a course which Professor Weldon, not recognizing the distinction between the varieties with opaque and transparent coats, himself wisely recommends. The coincidence of the peeled seeds giving simple Mendelian results is one which might have alarmed a critic less intrepid than Professor Weldon.

Bearing in mind, then, that the coats of peas may be transparent or opaque; and in the latter case may be variously pigmented, green, grey, reddish, purplish, etc.; that in any of the latter cases there may or may not be xenia; the reader will perceive that to use the statements of an author, whether scientific or lay, to the effect that on crossing varieties he obtained peas of such and such colours *without specifying at all whether the coats were transparent or whether the colours he saw were coat- or cotyledon-colours* is a proceeding fraught with peculiar and special risks.

(1) *Gärtner's cases.* Professor Weldon gives, as exceptions, a series of Gärtner's observations. Using several varieties, amongst them *Pisum sativum macrospermum*, a "grey" pea, with coloured flowers and seed-coats*, he obtained results partly Mendelian and partly, as now alleged, contradictory. The latter consist of seeds "dirty yellow" and "yellowish green," whereas it is suggested they should have been simply yellow.

Now students of this department of natural history will know that these same observations of Gärtner's, whether rightly or wrongly, have been doing duty for more than half a century as stock illustrations of xenia. In this

* Usually correlated characters, as Mendel knew.

capacity they have served two generations of naturalists. The ground nowadays may be unfamiliar, but others have travelled it before and recorded their impressions. Darwin, for example, has the following passage*:

"These statements led Gärtner, who was highly sceptical on the subject, carefully to try a long series of experiments; he selected the most constant varieties, and the results conclusively showed *that the colour of the skin of the pea* is modified when pollen of a differently coloured variety is used." (The italics are mine.)

In the true spirit of inquiry Professor Weldon doubtless reflected,

"'Tis not *Antiquity* nor *Author*,
That makes *Truth Truth*, altho' *Time's Daughter*";

but perhaps a word of caution to the reader that another interpretation exists would have been in place. It cannot be without amazement therefore that we find him appropriating these examples as referring to cotyledon-colour, with never a hint that the point is doubtful.

Giltay, without going into details, points out the ambiguity†. As Professor Weldon refers to the writings both of Darwin and Giltay, it is still more remarkable that he should regard the phenomenon as clearly one of cotyledon-colour and not coat-colour as Darwin and many other writers have supposed.

* *Animals and Plants*, 2nd ed. 1885, p. 428.

† "*Eine andere Frage ist jedoch, ob der Einfluss des Pollens auf den Keim schon äusserlich an diesen letzteren sichtbar sein kann. Darwin führt mehrere hierher gehörige Fälle an, und wahrscheinlich sind auch die Resultate der von Gärtner über diesen Gegenstand ausgeführten Experimente hier zu erwähnen, wenn es auch nicht ganz deutlich ist, ob der von Gärtner erwähnte directe Einfluss des Pollens sich nur innerhalb der Grenzen des Keimes merklich macht oder nicht.*" p. 490.

Without going further it would be highly improbable that Gärtner is speaking solely or even chiefly of the cotyledons, from the circumstance that these observations are given as evidence of "*the influence of foreign pollen on the female organs*"; and that Gärtner was perfectly aware of the fact that the coat of the seed was a maternal structure is evident from his statement to that effect on p. 80.

To go into the whole question in detail would require considerable space; but indeed it is unnecessary to labour the point. The reader who examines Gärtner's account with care, especially the peculiar phenomena obtained in the case of the "grey" pea (*macrospermum*), with specimens before him, will have no difficulty in recognizing that Gärtner is simply describing the seeds *as they looked in their coats*, and is not attempting to distinguish cotyledon-characters and coat-characters. If he had peeled them, which in the case of "grey" peas would be *absolutely necessary* to see cotyledon-colour, he must surely have said so.

Had he done so, he would have found the cotyledons full yellow in every ripe seed; for I venture to assert that anyone who tries, as we have, crosses between a yellow-cotyledoned "grey" pea, such as Gärtner's was, with any pure green variety will see that there is no question whatever as to absolute dominance of the yellow cotyledon-character here, more striking than in any other case. If exceptions are to be looked for, they will not be found *there*; and, except in so far as they show simple dominance of yellow, Gärtner's observations cannot be cited in this connection at all.

(2) *Seton's case.* Another exception given by Professor Weldon is much more interesting and instructive.

It is the curious case of Seton*. Told in the words of the critic it is as follows:—

"Mr Alexander Seton crossed the flowers of *Dwarf Imperial*, 'a well-known green variety of the Pea,' with the pollen of 'a white free-growing variety.' Four hybrid seeds were obtained, 'which did not differ in appearance from the others of the female parent.' These seeds therefore did *not* obey the law of dominance, or if the statement be preferred, greenness became dominant in this case. The seeds were sown, and produced plants bearing 'green' and 'white' seeds side by side in the same pod. An excellent coloured figure of one of these pods is given (*loc. cit.* Plate 9, Fig. 1), and is the only figure I have found which illustrates segregation of colours in hybrid Peas of the second generation."

Now if Professor Weldon had applied to this case the same independence of judgment he evinced in dismissing Darwin's interpretation of Gärtner's observations, he might have reached a valuable result. Knowing how difficult it is to give all the points in a brief citation, I turned up the original passage, where I find it stated that the mixed seeds of the second generation "were all completely either of one colour or the other, none of them having an intermediate tint, as Mr Seton had expected." The utility of this observation of the absence of intermediates, is that it goes some way to dispose of the suggestion of xenia as a cause contributing to the result.

Moreover, feeling perfectly clear, from the fact of the absence of intermediates, that the case must be one of simple dominance in spite of first appearances, I suggest the following account with every confidence that it is the true one. There have been several "*Imperials*,"

* Appendix to paper of Goss, *Trans. Hort. Soc.* v. 1822, pub. 1824 (*not* 1848, as given by Professor Weldon), p. 236.

though *Dwarf Imperial*, in a form which I can feel sure is Seton's form, I have not succeeded in seeing; but from Vilmorin's description that the peas when ripe are "*franchement verts*" I feel no doubt it was a green pea *with a green skin*. If it had had a transparent skin this description would be inapplicable. Having then a green skin, which may be assumed with every probability of truth, the seeds, even though the cotyledons were yellow, might, especially if examined fresh, be indistinguishable from those of the maternal type. Next from the fact of the mixture in the second generation we learn that the *semi-transparent seed-coat of the paternal form was dominant* as a plant-character, and indeed the coloured plate makes this fairly evident. It will be understood that this explanation is as yet suggestive, but from the facts of the second generation, any supposition that there was real irregularity in dominance in this case is out of the question*.

(3) *Tschermak's exceptions*. These are a much more acceptable lot than those we have been considering. Tschermak was thoroughly alive to the seed-coat question and consequently any exception stated as an unqualified fact on his authority must be accepted. The nature of these cases we shall see. Among the many varieties he used, some being *not* monomorphic, it would have been surprising if he had not found true irregularities in dominance.

(3 *a*) *Buchsbaum case*. This variety, growing in the open, gave once a pod in which *every seed but one was green*. In stating this case Professor Weldon refers to *Buchsbaum*

* Since the above passage was written I find the "*Imperials*" described in "Report of Chiswick Trials," *Proc. R. Hort. Soc.* 1860, I. p. 340, as "skin thick"; and on p. 360 "skin thick, blue"; which finally disposes of this "exception."

as "a yellow-seeded variety." Tschermak*, however, describes it as having "*gelbes, öfters gelblich-grünes Speichergewebe*" (cotyledons); and again says the cotyledon-colour is "*allerdings gerade bei Buchsbaum zur Spontanvariation nach gelb-grün neigend!*" The (!) is Tschermak's. Therefore Professor Weldon can hardly claim *Buchsbaum* as "yellow-seeded" without qualification.

Buchsbaum in fact is in all probability a blend-form and certainly not a true, stable yellow. One of the green seeds mentioned above grew and gave 15 *yellows* and three *greens*, and the result showed pretty clearly, as Tschermak says, that there had been an accidental cross with a tall green.

On another occasion *Telephone* ♀ (another impure green) × *Buchsbaum* gave four *yellow smooth and* two *green wrinkled*, but one [? both: the grammar is obscure] of the greens did not germinate†.

(3 *b*) *Telephone cases. Telephone*, crossed with at least one yellow variety (*Auvergne*) gave all or some green or greenish. These I have no doubt are good cases of "defective dominance" of yellow. But it must be noted that *Telephone is an impure green*. Nominally a green, it is as Professor Weldon has satisfied himself, very irregular in colour, having many intermediates shading to pure yellow and many piebalds. It is the variety from which alone Professor Weldon made his colour-scale. *I desire therefore to call special attention to the fact that Telephone, though*

* (36), p. 502 and (37), p. 663.

† Professor Weldon should have alluded to this. *Dead* seeds have no bearing on these questions, seeing that their characters may be pathological. The same seeds are later described as "*wie Telephone selbst*," so, apart from the possibility of death, they may also have been self-fertilised.

not a pure green, Tschermak's sample being as he says "gelblichweiss grün," a yellowish-white-green in cotyledon-colour, is the variety which has so far contributed the clearest evidence of the green colour dominating in its crosses with a yellow; and that *Buchsbaum* is probably a similar case. To this point we shall return. It may not be superfluous to mention also that one cross between *Fillbasket* (a thorough *green*) and *Telephone* gave three *yellowish* green seeds (Tschermak, (36), p. 501).

(3 *c*) *Couturier cases.* This fully yellow variety in crosses with two fully green sorts gave seeds either yellow or greenish yellow. In one case *Fillbasket* ♀ fertilised by *Couturier* gave mixed seeds, green and yellow. For any evidence to the contrary, the green in this case may have been self-fertilised. Nevertheless, taking the evidence together, I think it is most likely that *Couturier* is a genuine case of imperfect dominance of yellow. If so, it is the only true "exception" in crosses between stable forms.

We have now narrowed down Professor Weldon's exceptions to dominance of cotyledon-colour to two varieties, one yellow (*Couturier*), and one yellow "tending to green" (*Buchsbaum*), which show imperfect dominance of *yellow*; and one variety, *Telephone*, an impure and irregular green, which shows occasional but uncertain dominance of *green*.

What may be the meaning of the phenomenon shown by the unstable or mosaic varieties we cannot tell; but I venture to suggest that when we more fully appreciate the nature and genesis of the gametes, it will be found that the peculiarities of heredity seen in these cases have more in common with those of "false hybridism" (see p. 34) than with any true failure of dominance.

Before, however, feeling quite satisfied in regard even to this residuum of exceptions, one would wish to learn the subsequent fate of these aberrant seeds and how their offspring differed from that of their sisters. One only of them can I yet trace, viz. the green seed from *Telephone* ♀ × *Buchsbaum* ♂, which proved a veritable "green dominant." As for the remainder, Tschermak promises in his first paper to watch them. But in his second paper the only passage I can find relating to them declares that perhaps some of the questionable cases he mentioned in his first paper "*are attributable to similar isolated anomalies in dominance; some proved themselves by subsequent cultivation to be cases of accidental self-fertilisation; others failed to germinate**." I may warn those interested in these questions, that in estimating changes due to ripening, *dead* seeds are not available.

B. Seed-coats and shapes.

1. *Seed-coats.* Professor Weldon lays some stress on the results obtained by Correns† in crossing a pea having green cotyledons and a thin almost colourless coat (*grüne späte Erfurter Folger-erbse*) with two purple-flowered varieties. The latter are what are known in England as "grey" peas, though the term grey is not generally appropriate.

In these varieties the cotyledon-colour is yellow and

* "*Vielleicht sind einige der l.c.* 507 *bis* 508 *erwähnten fraglichen Fälle auf ähnliche vereinzelte Anomalien der Merkmalswerthigkeit zu beziehen; einige erwiesen sich allerdings beim Anbau als Producte ungewollter Selbstbefruchtung, andere keimten nicht.*"

† Regarding this case I have to thank Professor Correns for a good deal of information which he kindly sent me in response to my inquiry. I am thus able to supplement the published account in some particulars.

the coats are usually highly coloured or orange-brown. In reciprocal crosses Correns found no change from the maternal seed-coat-colour or seed-shape. On sowing these peas he obtained plants bearing peas which, using the terminology of Mendel and others, he speaks of as the "first generation."

These peas varied in the colour of their seed-coats from an almost colourless form slightly tinged with green like the one parent to the orange-brown of the other parent. The seeds varied in this respect not only from plant to plant, but from pod to pod, and from seed to seed, as Professor Correns has informed me.

The peas with more highly-coloured coats were sown and gave rise to plants with seeds showing the whole range of seed-coat-colours again.

Professor Weldon states that in this case neither the law of dominance nor the law of segregation was observed; and the same is the opinion of Correns, who, as I understand, inclines to regard the colour-distribution as indicating a "mosaic" formation. This is perhaps conceivable; and in that case the statement that there was no dominance would be true, and it would also be true that the unit of segregation, if any, was smaller than the individual plant and may in fact be the individual seed.

A final decision of this question is as yet impossible. Nevertheless from Professor Correns I have learnt one point of importance, namely, that the coats of all these seeds were *thick*, like that of the coloured and as usual dominant form. There is no "mosaic" of coats like one parent and coats like the other, though there may be a mosaic of colours. In regard to the distribution of *colour* however the possibility does not seem to me excluded that we are here dealing with changes influenced by conditions.

I have grown a "grey" pea and noticed that the seed-coats ripened in my garden differ considerably and not quite uniformly from those received from and probably ripened in France, mine being mostly pale and greyish, instead of reddish-brown. We have elsewhere seen (p. 120) that pigments of the seed-coat-colour may be very sensitive to conditions, and slight differences of moisture, for example, may in some measure account for the differences in colour. Among my crosses I have a pod of such "grey" peas fertilised by *Laxton's Alpha* (green cotyledons, coat transparent). It contained five seeds, of which four were *red-brown on one side* and grey with purple specks on the other. The fifth was of the grey colour on both sides. I regard this difference not as indicating segregation of character but merely as comparable with the difference between the two sides of a ripe apple, and I have little doubt that Correns' case may be of the same nature*. Phenomena somewhat similar to these will be met with in Laxton's case of the "maple" seeded peas (see p. 161).

2. *Seed-shapes.* Here Professor Weldon has three sets of alleged exceptions to the rule of dominance of round shape over wrinkled. The first are Rimpau's cases, the second are Tschermak's cases, the third group are cases of "grey" peas, which we will treat in a separate section (see pp. 153 and 158).

(*a*) *Rimpau's cases.* Professor Weldon quotes Rimpau as having crossed wrinkled and round peas† and found

* Mr Hurst, of Burbage, tells me that in varieties having coats green or white, e.g. *American Wonder*, the white coats are mostly from early, the green from later pods, the tints depending on conditions and exposure.

† In the first case *Knight's Marrow* with *Victoria*, both ways; in the second *Victoria* with *Telephone*, both ways.

the second hybrid generation dimorphic as usual. The wrinkled peas were selected and sown and gave wrinkled peas *and round* peas, becoming "true" to the wrinkled character in one case only in the fifth year, while in the second case—that of a *Telephone* cross—there was a mixture of round and wrinkled similarly resulting from *wrinkled* seed for two years, but the experiment was not continued.

These at first sight look like genuine exceptions. In reality, however, they are capable of a simple explanation. It must be remembered that Rimpau was working in ignorance of Mendel's results, was not testing any rule, and was not on the look out for irregularities. Now all who have crossed wrinkled and round peas on even a moderate scale will have met with the fact that there is frequently *some* wrinkling in the cross-bred seeds. Though round when compared with the true wrinkled, these are often somewhat more wrinkled than the round type, and in irregular degrees. For my own part I fully anticipate that we may find rare cases of complete blending in this respect though I do not as yet know one.

Rimpau gives a photograph of eight peas (Fig. 146) which he says represent the wrinkled form derived from this cross. It is evident that these are not from *one pod* but a miscellaneous selection. On close inspection it will be seen that while the remainder are shown with their *cotyledon*-surfaces upwards, the two peas at the lower end of the row are represented with their *hilar*-surfaces upwards. Remembering this it will be recognized that these two lower peas are in fact *not* fully wrinkled peas but almost certainly *round* "hybrids," and the depression is merely that which is often seen in round peas (such as *Fillbasket*), squared by mutual pressure. Such peas, when sown, might of course give some round.

As Tschermak writes ((37), p. 658), experience has shown him that cross-bred seeds with character transitional between "round" and "wrinkled" behave as hybrids, and have both wrinkled and round offspring, and he now reckons them accordingly with the round dominants.

Note further the fact that Rimpau found the wrinkled form came true in the *fifth* year, while the round gave at first more, later fewer, wrinkleds, not coming true till the *ninth* year. This makes it quite clear that there *was* dominance of the round form, but that the heterozygotes were not so sharply distinguishable from the two pure forms as to be separated at once by a person not on the look-out for the distinctions. Nevertheless there *was* sufficient difference to lead to a practical distinction of the cross-breds both from the pure dominants and from the pure recessives.

The *Telephone* case may have been of the same nature; though, as we have seen above, this pea is peculiar in its colour-heredity and may quite well have followed a different rule in shape also. As stated before, the wrinkled offspring were not cultivated after the third year, but the *round* seeds are said to have still given some wrinkleds in the eighth year after the cross, as would be expected in a simple Mendelian case.

(*b*) *Tschermak's cases.* The cases Professor Weldon quotes from Tschermak all relate to crosses with *Telephone* again, and this fact taken with the certainty that the colour-heredity of *Telephone* is abnormal makes it fairly clear that there is here something of a really exceptional character. What the real nature of the exception is, and how far it is to be taken as contradicting the "law of dominance," is quite another matter.

3. *Other phenomena, especially regarding seed-shapes, in the case of "grey" peas. Modern evidence.* Professor Weldon quotes from Tschermak the interesting facts about the "grey" pea, *Graue Riesen*, but does not attempt to elucidate them. He is not on very safe ground in adducing these phenomena as conflicting with the "law of dominance." Let us see whither we are led if we consider these cases. On p. 124 I mentioned that the classes round and wrinkled do not properly hold if we try to extend them to large-seeded sorts, and that these cases require separate consideration. In many of such peas, which usually belong either to the classes of sugar-peas (*mange-touts*) or "grey" peas (with coloured flowers), the seeds would be rather described as irregularly indented, lumpy or stony*, than by any use of the terms round or wrinkled. One sugar-pea (*Debarbieux*) which I have used has large flattish, smooth, yellow seeds with white skins, and this also in its crossings follows the rules about to be described for the large-seeded "grey" peas.

In the large "grey" peas the most conspicuous feature is the seed-coat, which is grey, brownish, or of a bright reddish colour. Such seed-coats are often speckled with purple, and on boiling these seed-coats turn dark brown. They are in fact the very peas used by Mendel in making up his third pair of characters. Regarding them Professor

* Gärtner's *macrospermum* was evidently one of these, though from the further account (p. 498) it was probably more wrinkled. There are of course *mange-touts* which have perfectly round seeds. Mendel himself showed that the *mange-tout* character, the soft constricted pod, was transferable. There are also *mange-touts* with fully wrinkled seeds and "grey" peas with small seeds (see Vilmorin-Andrieux, *Plantes Potagères*, 1883).

Weldon, stating they may be considered separately, writes as follows:—

"Tschermak has crossed *Graue Riesen* with five races of *P. sativum*, and he finds that the form of the first hybrid seeds *follows the female parent*, so that if races of *P. sativum* with round smooth seeds be crossed with *Graue Riesen* (which has flattened, feebly wrinkled seeds) the hybrids will be round and smooth or flattened and wrinkled, as the *P. sativum* or the *Graue Riesen* is used as female parent*. There is here a more complex phenomenon than at first sight appears; because if the flowers of the first hybrid generation are self-fertilised, the resulting seeds of the second generation invariably resemble those of the *Graue Riesen* in shape, although in colour they follow Mendel's law of segregation!"

From this account who would not infer that we have here some mystery which does not accord with the Mendelian principles? As a matter of fact the case is dominance in a perfectly obvious if distinct form.

Graue Riesen, a large grey sugar-pea, the *pois sans parchemin géant* of the French seedsmen, has full-yellow cotyledons and a highly coloured seed-coat of varying tints. In shape the seed is somewhat flattened with irregular slight indentations, lightly wrinkled if the term be preferred. Tschermak speaks of it in his first paper as "*Same flach, zusammengedrückt*"—a flat, compressed seed; in his second paper as "*flache, oft schwach gerunzelte Cotyledonen-form,*" or cotyledon-shape, flat, often feebly wrinkled, as Professor Weldon translates.

First-crosses made from this variety, each with a different form of *P. sativum*, are stated on the authority of Tschermak's five cases, to follow exclusively the maternal seed-shape. From "*schwach gerunzelte,*" "feebly wrinkled," Professor Weldon easily passes to "wrinkled," and tells us

* Correns found a similar result.

that according as a round *sativum* or the *Graue Riesen* is used as mother, the first-cross seeds "will be round and smooth or flattened and wrinkled."

As a matter of fact, however, the seeds of *Graue Riesen* though *slightly* wrinkled do not belong to the "wrinkled" class; but if the classification "wrinkled" and "round" is to be extended to such peas at all, they belong to the *round*. Mendel is careful to state that his *round* class are "either spherical or roundish, the depressions on the surface, when there are any, always slight"; while the "wrinkled" class are "irregularly angular, deeply wrinkled*."

On this description alone it would be very likely that *Graue Riesen* should fall into the *round* class, and as such it behaves in its crosses, *being dominant over wrinkled* (see Nos. 3 and 6, below). I can see that in this case Professor Weldon has been partly misled by expressions of Tschermak's, but the facts of the second generation should have aroused suspicion. Neither author notices that as all five varieties crossed by Tschermak with *Graue Riesen* were *round*, the possibilities are not exhausted. Had Tschermak tried a really wrinkled *sativum* with *Graue Riesen* he would have seen this obvious explanation.

As some of my own few observations of first-crosses bear on this point I may quote them, imperfect though they are.

I grew the purple-flowered sugar-pea "*Pois sans parchemin géant à très large cosse,*" a soft-podded "*mangetout*" pea, flowers and seed-coats coloured, from Vilmorin's, probably identical with *Graue Riesen.*

1. One flower of this variety fertilised with *Pois très nain de Bretagne* (very small seed; yellow cotyledons; very

* "*Entweder kugelrund oder rundlich, die Einsenkungen, wenn welche an der Oberfläche vorkommen, immer nur seicht, oder sie sind unregelmässig kantig, tief runzlig (P. quadratum).*"

round) gave seven seeds indistinguishable (in their coats) from those of the mother, save for a doubtful increase in purple pigmentation of coats.

2. Fertilised by *Laxton's Alpha* (green; wrinkled; coats transparent), two flowers gave 11 seeds exactly as above, the purple being in this case clearly increased.

In the following the purple sugar-pea was *father*.

3. *Laxton's Alpha* (green; wrinkled; coats transparent) fertilised by the purple sugar-pea gave one pod of four seeds with yellow cotyledons and *round* form.

4. *Fillbasket* (green; smooth but squared; coats green) fertilised by the *purple* sugar-pea gave one pod with six seeds, yellow cotyledons*; *Fillbasket* size and shape; but the normally green coat yellowed near *the hilum* by xenia.

5. *Express* ("blue"-green cotyledons and transparent skins; round) fertilised with *purple sugar*-pea gave one pod with four seeds, yellow cotyledons, shape round, much as in *Fillbasket*.

6. *British Queen* (yellow cotyledons, wrinkled, white coats) ♀ × purple sugar-pea gave two pods with seven seeds, cotyledons yellow, coats *tinged greenish* (xenia?), all *round*.

So much for the "*Purple*" sugar-pea.

I got similar results with *Mange-tout Debarbieux*. This is a soft-podded *Mange-tout* or sugar-pea, with white flowers, large, flattish, smooth seeds, scarcely dimpled; yellow cotyledons.

* The colour is the peculiarly deep yellow of the "grey" *mange-tout*.

7. *Debarbieux* fertilised by *Serpette nain blanc* (yellow cotyledons; wrinkled; white skin; dwarf) gave one pod with six seeds, size and shape of *Debarbieux*, with slight dimpling.

8. *Debarbieux* by *nain de Bretagne* (very small; yellow cotyledons; very round) gave three pods, 12 seeds, all yellow cotyledons, of which two pods had eight seeds identical in shape with *Debarbieux*, while the third had four seeds like *Debarbieux* but more dimpled. The reciprocal cross gave two seeds exactly like *nain de Bretagne*.

But it may be objected that the shape of this large grey pea is very peculiar*; and that it maintains its type remarkably when fertilised by many distinct varieties though its pollen effects little or no change in them; for, so long as round varieties of *sativum* are used as mothers, this is true as we have seen. But when once it is understood that in *Graue Riesen* there is no question of wrinkling, seeing that the variety behaves as a *round* variety, the shape and especially the size of the seed must be treated as a maternal property.

Why the distinction between the shape of *Graue Riesen* and that of ordinary round peas should be a matter of maternal physiology we do not know. The question is one for the botanical chemist. But there is evidently very considerable regularity, the seeds borne by the *cross-breds* exhibiting the form of the "grey" pea, which is then a dominant character as much as the seed-coat characters

* It is certainly subject to considerable changes according to conditions. Those ripened in my garden are without exception much larger and flatter than Vilmorin's seeds (now two years old) from which they grew. The colour of the coats is also much duller. These changes are just what is to be expected from the English climate—taken with the fact that my sample of this variety was late sown.

are. And that is what Tschermak's *Graue Riesen* crosses actually did, thereby exhibiting dominance in a very clear form. To interject these cases as a mystery without pointing out how easily they can be reconciled with the "law of dominance" may throw an unskilled reader into gratuitous doubt.

Finally, since *the wrinkled peas, Laxton's Alpha* and *British Queen, pollinated by a large flat mange-tout, witness Nos.* 3 *and* 6 *above*, became round in both cases where this experiment was made, we here merely see the usual dominance of the non-wrinkled character; though of course if a *round*-seeded mother be used there can be no departure from the maternal shape, as far as roundness is concerned.

Correns' observations on the shapes of a "grey" pea crossed with a round shelling pea, also quoted by Professor Weldon as showing no dominance of roundness, are of course of the same nature as those just discussed.

C. *Evidence of Knight and Laxton.*

In the last two sections we have seen that in using peas of the "grey" class, i.e. with brown, red, or purplish coats, special phenomena are to be looked for, and also that in the case of large "indented" peas, the phenomena of size and shape may show some divergence from that simple form of the phenomenon of dominance seen when ordinary round and wrinkled are crossed. Here the fuller discussion of these phenomena must have been left to await further experiment, were it not that we have other evidence bearing on the same questions.

The first is that of Knight's well-known experiments, long familiar but until now hopelessly mysterious. I have not space to quote the various interpretations which Knight and others have put upon them, but as the Mendelian principle at once gives a complete account of the whole, this is scarcely necessary, though the matter is full of historical interest.

Crossing a white pea with a very large grey purple-flowered form Knight (21) found that the peas so produced "were not in any sensible degree different from those afforded by other plants of the same [white] variety; owing, I imagine, to the external covering of the seed (as I have found in other plants) being furnished entirely by the female*." All grew very tall†, and had colours of male parent‡. The seeds they produced were dark grey§.

"I had frequent occasion to observe, in this plant [the hybrid], a stronger tendency to produce purple blossoms, and coloured seeds, than white ones; for when I introduced the farina of a purple blossom into a white one, the whole of the seeds in the succeeding year became coloured [viz. $DR \times D$ giving DD and DR]; but, when I endeavoured to discharge this colour, by reversing the process, a part only of them afforded plants with white blossoms; this part sometimes occupying one end of the pod, and being at times irregularly intermixed with those which, when sown, retained their colour" [viz. $DR \times R$ giving DR and RR] (draws conclusions, now obviously erroneous‖).

In this account we have nothing not readily intelligible in the light of Mendel's hypothesis.

The next evidence is supplied by an exceptionally complete record of a most valuable experiment made by

* Thus avoiding the error of Seton, see p. 144. There is no xenia perhaps because the seed-coat of mother was a transparent coat.

† As heterozygotes often do.

‡ Dominance of the purple form.

§ Dominance of the grey coat as a maternal character.

‖ Sherwood's view (*J. R. Hort. Soc.* XXII. p. 252) that this was the origin of the "Wrinkled" pea, seems very dubious.

Laxton*. The whole story is replete with interest, and as it not only carries us on somewhat beyond the point reached by Mendel, but furnishes an excellent illustration of how his principles may be applied, I give the whole account in Laxton's words, only altering the paragraphing for clearness, and adding a commentary. The paper appears in *Jour. Hort. Soc.* N.S. III. 1872, p. 10, and very slightly abbreviated in *Jour. of Hort.* XVIII. 1870, p. 86. Some points in the same article do not specially relate to this section, but for simplicity I treat the whole together.

It is not too much to say that two years ago the whole of this story would have been a maze of bewildering confusion. There are still some points in it that we cannot fully comprehend, for the case is one of far more than ordinary complexity, but the general outlines are now clear. In attempting to elucidate the phenomena it will be remembered that there are no statistics (those given being inapplicable), and the several offspring are only imperfectly referred to the several classes of seeds. This being so, our rationale cannot hope to be complete. Laxton states that as the seeds of peas are liable to change colour with keeping, for this and other reasons he sent to the Society a part of the seeds resulting from his experiment before it was brought to a conclusion.

"The seeds exhibited were derived from a single experiment. Amongst these seeds will be observed some of several remarkable colours, including black, violet, purple-streaked and spotted, maple, grey, greenish, white, and almost every intermediate tint, the varied colours being apparently produced on the outer coat or envelope of the cotyledons only.

* It will be well known to all practical horticulturalists that Laxton, originally of Stamford, made and brought out a large number of the best known modern peas. The firm is now in Bedford.

The peas were selected for their colours, &c., from the third year's sowing in 1869 of the produce of a cross in 1866 of the early round white-seeded and white-flowered garden variety "Ringleader," which is about 2½ ft. in height, fertilised by the pollen of the common purple-flowered "maple" pea, which is taller than "Ringleader," and has slightly indented seeds. I effected impregnation by removing the anthers of the seed-bearer, and applying the pollen at an early stage. This cross produced a pod containing five round white peas, exactly like the ordinary "Ringleader" seeds*.

In 1867 I sowed these seeds, and all five produced tall purple-flowered purplish-stemmed plants†, and the seeds, with few exceptions, had all maple or brownish-streaked envelopes of various shades; the remainder had entirely violet or deep purple-coloured envelopes‡: in shape the peas were partly in-

* A round white ♀ × grey ♂ giving the usual result, round, "white" (yellow) seeds.

† Tall heterozygotes, with normal dominance of purple flowers.

‡ Here we see dominance of the *pigmented* seed-coat as a maternal character over *white* seed-coat. The colours of the seed-coats are described as essentially two: maple or brown-streaked, and violet, the latter being a small minority. As the sequel shows, the latter are heterozygotes, not breeding true. Now Mendel found, and the fact has been confirmed both by Correns and myself, that crossing a grey pea which is capable of producing purple leads to such production as a form of xenia.

We have here therefore in the purple seeds the union of dissimilar gametes, with production of xenia. But as the brown-streaked seeds are also in part heterozygous, the splitting of a compound allelomorph has probably taken place, though without precise statistics and allotment of offspring among the several seeds the point is uncertain. The colour of seed-coats in "grey" peas and probably "maples" also is, as was stated on p. 150, sensitive to conditions, but the whole difference between "maples" and purple is too much to attribute safely to such irregularity. "Maple" is the word used to describe certain seed-coats which are pigmented with intricate brown mottlings on a paler buff ground. In French they are *perdrix*.

dented; but a few were round*. Some of the plants ripened off earlier than the "maple," which, in comparison with "Ringleader," is a late variety; and although the pods were in many instances partially abortive, the produce was very large†.

In 1868 I sowed the peas of the preceding year's growth, and selected various plants for earliness, productiveness, &c. Some of the plants had light-coloured stems and leaves; these all showed white flowers, and produced round white seeds‡. Others had purple flowers, showed the purple on the stems and at the axils of the stipules, and produced seeds with maple, grey, purple-streaked, or *mottled, and a few only, again, with violet*-coloured envelopes. Some of the seeds were round, some partially indented §. The pods on each plant, in the majority of instances, contained peas of like characters; but in a few cases the peas in the same pod varied slightly, and in some instances a pod or two on the same plant contained seeds all distinct from the remainder||. The white-flowered plants were generally dwarfish,

* This is not, as it stands, explicable. It seems from this point and also from what follows that if the account is truly given, some of the plants may have been mosaic with segregation of characters in *particular flowers ; but see subsequent note.*

† As, commonly, in heterozygotes when fertile.

‡ Recessive in flower-colour, seed-coat colour, and in seed-shape as a maternal character: pure recessives as the sequel proved.

§ These are then a mixture of pure dominants and cross-bred dominants, and are now inextricably confused. This time the round seeds may have been all on particular plants—showing recessive seed-shape as a maternal character. It seems just possible that this fact suggested the idea of "round" seeds on the *coloured* plants in the last generation. Till that result is confirmed it should be regarded as very doubtful on the evidence. But we cannot at the present time be sure how much difference there was between these *round* seeds and the *normal* maples in point of shape; and on the whole it seems most probable that the roundness was a mere fluctuation, such as commonly occurs among the peas with large indented seeds.

|| Is this really evidence of segregation of characters, the flower

of about the height of "Ringleader"; but the coloured-flowered sorts varied altogether as to height, period of ripening, and colour and shape of seed*. Those seeds with violet-coloured envelopes produced nearly all maple- or parti-coloured seeds, and only here and there one with a violet-coloured envelope; that colour, again, appeared only incidentally, and in a like degree in the produce of the maple-coloured seeds†.

In 1869 the seeds of various selections of the previous year were again sown separately; and the white-seeded peas again produced only plants with white flowers and round white seeds‡. Some of the coloured seeds, which I had expected would produce purple-flowered plants, produced plants with white flowers and round white seeds only§; the majority, however, brought plants with purple flowers and with seeds principally marked with purple or grey, the maple- or brown-streaked being in the minority‖. On some of the purple-flowered plants were again a few pods with peas differing entirely from the remainder on the same plant. In some pods the seeds were all white, in others all black, and in a few, again, all violet¶; but those plants which bore maple-coloured seeds seemed the most constant and fixed in character of the purple-flowered seedlings**, and the purplish and grey peas, being of intermediate characters, ap-

being the unit? In any case the possibility makes the experiment well worth repeating, especially as Correns has seen a phenomenon conceivably similar.

* Being a mixture of heterozygotes (probably involving several pairs of allelomorphs) and homozygotes.

† This looks as if the violet colour was merely due to irregularity of xenia.

‡ Pure recessives.

§ Pure recessives in coats showing maternal dominant character.

‖ Now recognized as pure homozygotes.

¶ This seems almost certainly segregation by flower-units, and is as yet inexplicable on any other hypothesis. Especially paradoxical is the presence of "white" seeds on these plants. The impression is scarcely resistible that some remarkable phenomenon of segregation was really seen here.

** Being now homozygotes.

peared to vary most*. The *violet-coloured seeds again produced* almost invariably purplish, grey, or maple peas, the clear violet colour only now and then appearing, either wholly in one pod or on a single pea or two in a pod. All the seeds of the purple-flowered plants were again either round or only partially indented; and the plants varied as to height and earliness. In no case, however, does there seem to have been an intermediate-coloured flower; for although in some flowers I thought I found the purple of a lighter shade, I believe this was owing to light, temperature, or other circumstances, and applied equally to the parent maple. I have never noticed a single tinted white flower nor an indented white seed in either of the three years' produce. The whole produce of the third sowing consisted of seeds of the colours and in the approximate quantities in order as follows,—viz.: 1st, white, about half; 2nd, purplish, grey, and violet (intermediate colours), about three-eighths; and, 3rd, maple, about one-eighth.

From the above I gather that the white-flowered white-seeded pea is (if I may use the term) an original variety well fixed and distinct entirely from the maple, that the two do not thoroughly intermingle (for whenever the white flower crops out, the plant and its parts all appear to follow exactly the characters of the white pea), and that the maple is a cross-bred variety which has become somewhat permanent and would seem to include amongst its ancestors one or more bearing seeds either altogether or partly violet- or purple-coloured; for although this colour does not appear on the seed of the "maple," it is very potent in the variety, and appears in many parts of the plant and its offspring from cross-fertilised flowers, sometimes on the external surface or at the sutures of the pods of the latter, at others on the seeds and stems, and very frequently on the seeds; and whenever it shows itself on any part of the plant, the flowers are invariably purple. My deductions have been confirmed by intercrosses effected between the various white-, blue-, some singularly bright green-seeded peas which I have selected, and the maple- and purple-podded and the purple-flowered sugar peas, and by reversing those crosses.

* Being heterozygotes exclusively.

I have also deduced from my experiments, in accordance with the conclusions of the late Mr Knight and others, that the colours of the envelopes of the seeds of peas immediately resulting from a cross are never changed*. I find, however, that the colour and probably the substance of the cotyledons are sometimes, but not always, changed by the cross fertilisation of two different varieties; and I do not agree with Mr Knight that the form and size of the seeds produced are unaltered†; for I have on more than one occasion observed that the cotyledons in the seeds directly resulting from a cross of a blue wrinkled pea fertilised by the pollen of a white round variety have been of a greenish-white colour‡, and the seeds nearly round§ and larger or smaller according as there may have been a difference in the size of the seeds of the two varieties||.

I have also noticed that a cross between a round white and a blue wrinkled pea will in the third and fourth generations (second and third years' produce) at times bring forth blue round, blue wrinkled, white round and white wrinkled peas in the same pods, that the white round seeds, when again sown, will produce only white round seeds, that the white wrinkled seeds will, up to the fourth or fifth generation, produce both blue and white wrinkled and round peas, that the blue round peas will produce blue wrinkled and round peas, but that the blue wrinkled peas will bear only blue wrinkled seeds¶. This

* The nature of this mistake is now clear; for as stated above xenia is only likely to occur when the maternal seed-coat is pigmented. The violet coats in this experiment are themselves cases of xenia.

† Knight, it was seen, crossed round ♀ × indented ♂ and consequently got no change of form.

‡ Cotyledons seen through coat.

§ Ordinary dominance of round.

|| This is an extraordinary statement to be given as a general truth. There are sometimes indications of this kind, but certainly the facts are not usually as here stated.

¶ If we were obliged to suppose that this is a matured conclusion based on detailed observation it would of course constitute the most serious "exception" yet recorded. But it is clear that the five *would seem to indicate that the white round and the blue* wrinkled peas are distinct varieties derived from ancestors respectively possessing one only of those marked qualities; and, in my opinion, the white round peas trace their origin to a dwarfish pea having white flowers and round white seeds, and the blue wrinkled varieties to a tall variety, having also white flowers but blue wrinkled seeds. It is also noticeable, that from a single cross between two different peas many hundreds of varieties, not only like one or both parents and intermediate, but apparently differing from either, may be produced in the

statements are not mutually consistent. We have dominance of round white in first cross.

In the second generation blue wrinkled give only blue wrinkled, and blue round give blue wrinkled and round, in accordance with general experience. But we are told that white round give *only* white round. This would be true of some white rounds, but not, according to general experience, of all. Lastly we are told *white wrinkled give all four classes.* If we had not been just told by Laxton that the first cross showed dominance of white round, and that blue wrinkled and blue round give the Mendelian result, I should hesitate in face of this positive statement, but as it is inconsistent with the rest of the story I think it is unquestionably an error of statement. The context, and the argument based on the maple crosses show clearly also what was in Laxton's mind. He plainly expected the characters of the original pure varieties to separate out according to their original combinations, and this expectation confused his memory and general impressions. This, at least, until any such result is got by a fresh observer, using strict methods, is the only acceptable account.

Of the same nature is the statement given by the late Mr Masters to Darwin (*Animals and Plants*, I. p. 318) that blue round, white round, blue wrinkled, and white wrinkled, all reproduced all four sorts during successive years. Seeing that one sort would give all four, and two would give two kinds, without special counting such an impression might easily be produced. There are the further difficulties due to seed-coat colour, and the fact that the distinction between round and wrinkled may need some discrimination. The sorts are not named, and the case cannot be further tested.

course of three or four years (the shortest time which I have ascertained it takes to attain the climax of variation in the produce of cross-fertilised peas, and until which time it would seem useless to expect a fixed seedling variety to be produced*), although a reversion to the characters of either parent, or of any one of the ancestors, may take place at an earlier period.

These circumstances do not appear to have been known to Mr Knight, as he seems to have carried on his experiments by continuing to cross his seedlings in the year succeeding their production from a cross and treating the results as reliable; whereas it is probable that the results might have been materially affected by the disturbing causes then in existence arising from the previous cross fertilisation, and which, I consider, would, in all cases where either parent has not become fixed or permanent, lead to results positively perplexing and uncertain, and to variaations almost innumerable. I have again selected, and intend to sow, watch, and report; but as the usual climax of variation is nearly reached in the recorded experiment, I do not anticipate much further deviation, except in height and period of ripening—characters which are always very unstable in the pea. There are also important botanical and other variations and changes occurring in cross-fertilised peas to which it is not my province here to allude; but in conclusion I may, perhaps, in furtherance of the objects of this paper, be permitted to inquire whether any light can, from these observations or other means, be thrown upon the origin of the cultivated kinds of peas, especially the "maple" variety, and also as to the source whence the violet and other colours which appear at intervals on the seeds and in the offspring of cross-fertilised purple-flowered peas are derived."

The reader who has closely followed the preceding passage will begin to appreciate the way in which the new principles help us to interpret these hitherto paradoxical phenomena. Even in this case, imperfectly recorded as it is, we can form a fairly clear idea of what was taking place.

* See later.

If the "round" seeds really occurred as a distinct class, on the heterozygotes as described, it is just possible that the fact may be of great use hereafter.

We are still far from understanding maternal seed-form—and perhaps size—as a dominant character. So far, as Miss Saunders has pointed out to me, it appears to be correlated with a thick and coloured seed-coat.

We have now seen the nature of Professor Weldon's collection of contradictory evidence concerning dominance in peas. He tells us: "Enough has been said to show the grave discrepancy between the evidence afforded by Mendel's experiments and that obtained by observers equally trustworthy."

He proceeds to a discussion of the *Telephone* and *Telegraph* group and recites facts, which I do not doubt for a moment, showing that in this group of peas—which have unquestionably been more or less "blend" or "mosaic" forms from their beginning—the "laws of dominance and segregation" do not hold. Professor Weldon's collection of the facts relating to *Telephone*, &c. has distinct value, and it is the chief addition he makes to our knowledge of these phenomena. The merit however of this addition is diminished by the erroneous conclusion drawn from it, as will be shown hereafter. Meanwhile the reader who has studied what has been written above on the general questions of stability, "purity," and "universal" dominance, will easily be able to estimate the significance of these phenomena and their applicability to Mendel's hypotheses.

D. Miscellaneous cases in other plants and animals.

Professor Weldon proceeds:

"In order to emphasize the need that the ancestry of the parents, used in crossing, should be considered in discussing the results of a cross, it may be well to give one or two more examples of fundamental inconsistency between different competent observers."

The "one or two" run to three, viz. Stocks (hoariness and colour); *Datura* (character of fruits and colour of flowers); and lastly colours of Rats and Mice. Each of these subjects, as it happens, has been referred to in the forthcoming paper by Miss Saunders and myself. *Datura* and *Matthiola* have been subjected to several years' experiment and I venture to refer the reader who desires to see whether the facts are or are not in accord with Mendel's expectation and how far there is "fundamental inconsistency" amongst them to a perusal of our work.

But as Professor Weldon refers to some points that have not been explicitly dealt with there, it will be safer to make each clear as we proceed.

1. *Stocks* (*Matthiola*). Professor Weldon quotes Correns' observation that glabrous Stocks crossed with hoary gave offspring all hoary, while Trevor Clarke thus obtained some hoary and some glabrous. As there are some twenty different sorts of Stocks* it is not surprising that different observers should have chanced on different materials and obtained different results. Miss Saunders

* The number in Haage and Schmidt's list exceeds 200, counting colour-varieties.

has investigated laws of heredity in Stocks on a large scale and an account of her results is included in our forthcoming Report. Here it must suffice to say that the cross hoary ♀ × glabrous ♂ always gave offspring all hoary except once: that the cross glabrous ♀ × hoary ♂ of several types gave all hoary; *but* the same cross using other hoary types did frequently give a mixture, some of the offspring being hoary, others glabrous. Professor Weldon might immediately decide that here was the hoped for phenomenon of "reversed" dominance, due to ancestry, but here again that hypothesis is excluded. For the glabrous (recessive) cross-breds were *pure*, and produced on self-fertilisation glabrous plants only, being in fact, almost beyond question, "false hybrids" (see p. 34), a specific phenomenon which has nothing to do with the question of dominance.

Professor Weldon next suggests that there is discrepancy between the observations as to flower-colour. He tells us that Correns found *violet* Stocks crossed with "*yellowish white*" gave violet or shades of violet flaked together. According to Professor Weldon

"On the other hand Nobbe crossed a number of varieties of *M. annua* in which the flowers were white, violet, carmine-coloured, crimson or dark blue. These were crossed in various ways, and before a cross was made the colour of each parent was matched by a mixture of dry powdered colours which was preserved. In every case the hybrid flower was of an intermediate colour, which could be matched by mixing the powders which recorded the parental colours. The proportions in which the powders were mixed are not given in each [any] case, but it is clear that the colours blended*."

* The original passage is in *Landwirths. Versuchstationen*, 1888, XXXV. [*not* XXXIV.], p. 151.

On comparing Professor Weldon's version with the originals we find the missing explanations. Having served some apprenticeship to the breeding of Stocks, we, here, are perhaps in a better position to take the points, but it is to me perfectly inexplicable how in such a simple matter as this he can have gone wrong.

Note then

(1) That Nobbe does *not* specify *which* colours he crossed together, beyond the fact that *white* was crossed with each fertile form. The *crimson* form (*Karmoisinfarbe*), being double to the point of sterility, was not used. There remain then, white, carmine, and two purples (violet, "dark blue"). When *white* was crossed with either of these, Nobbe says the colour becomes *paler*, whichever sort gave the pollen. Nobbe does not state that he crossed *carmine* with the purples.

(2) Professor Weldon gives no qualification in his version. Nobbe however states that he found it very difficult to distinguish the result of crossing *carmine with white* from that obtained by crossing *dark blue or violet with white**, thereby nullifying Professor Weldon's statement that in every case the cross was a simple mixture of the parental colours—a proposition sufficiently disproved by Miss Saunders' elaborate experiments.

(3) Lately the champion of the "importance of small variations," Professor Weldon now prefers to treat the distinctions between established varieties as negligible

* *"Es ist sogar sehr schwierig, einen Unterschied in der Farbe der Kreuzungsprodukte von Karmin und Weiss gegenüber Dunkelblau oder Violett und Weiss zu erkennen."*

fluctuations instead of specific phenomena*. Therefore when Correns using "*yellowish white*" obtained one result and Nobbe using "*white*" obtained another, Professor Weldon hurries to the conclusion that the results are comparable and therefore contradictory. Correns however though calling his flowers *gelblich-weiss* is careful to state that they are described by Haage and Schmidt (the seed-men) as "*schwefel-gelb*" or sulphur-yellow. The topics Professor Weldon treats are so numerous that we cannot fairly expect him to be personally acquainted with all; still had he *looked* at Stocks before writing, or even at the literature relating to them, he would have easily seen that these yellow Stocks are a thoroughly distinct form†; and in accordance with this fact it would be surprising if they had not a distinctive behaviour in their crosses. To use our own terminology their colour character depends almost certainly on a *compound* allelomorph. Consequently there is no evidence of contradiction in the results, and appeal to ancestry is as unnecessary as futile.

2. *Datura*. As for the evidence on *Datura*, I must refer the reader again to the experiments set forth in our Report.

The phenomena obey the ordinary Mendelian rules with accuracy. There are (as almost always where discontinuous

* See also the case of *Buchsbaum*, p. 146, which received similar treatment.

† One of the peculiarities of most *double* "sulphur" races is that the singles they throw are *white*. See Vilmorin, *Fleurs de pleine Terre*, 1866, p. 354, *note*. In *Wien. Ill. Gartenztg*. 1891, p. 74, mention is made of a new race with singles also "sulphur," cp. *Gartenztg*. 1884, p. 46. Messrs Haage and Schmidt have kindly written to me that this new race has the alleged property, but that six other yellow races (two distinct colours) throw their singles white.

variation is concerned) occasional cases of "mosaics," a phenomenon which has nothing to do with "ancestry."

3. *Colours of Rats and Mice.* Professor Weldon reserves his collection of evidence on this subject for the last. In it we reach an indisputable contribution to the discussion—a reference to Crampe's papers, which together constitute without doubt the best evidence yet published, respecting colour-heredity in an animal. So far as I have discovered, the only previous reference to these memoirs is that of Ritzema Bos*, who alludes to them in a consideration of the alleged deterioration due to in-breeding.

Now Crampe through a long period of years made an exhaustive study of the peculiarities of the colour-forms of Rats, white, black, grey and their piebalds, as exhibited in Heredity.

Till the appearance of Professor Weldon's article Crampe's work was unknown to me, and all students of Heredity owe him a debt for putting it into general circulation. My attention had however been called by Dr Correns to the interesting results obtained by von Guaita, experimenting with crosses originally made between albino *mice* and piebald Japanese waltzing mice. This paper also gives full details of an elaborate investigation admirably carried out and recorded.

In the light of modern knowledge both these two researches furnish material of the most convincing character demonstrating the Mendelian principles. It would be a useful task to go over the evidence they contain and rearrange it in illustration of the laws now perceived. To do this here is manifestly impossible, and it must suffice to point out that the albino is a simple recessive in both cases (the

* *Biol. Cblt.* XIV. 1894, p. 79.

waltzing character in mice being also a recessive), and that the "wild grey" form is one of the commonest heterozygotes —there appearing, like the yellow cotyledon-colour of peas, *in either of two capacities*, i.e. as a pure form, or as the heterozygote form of one or more combinations*.

Professor Weldon refers to both Crampe and von Guaita, whose results show an essential harmony in the fact that both found *albino* an obvious recessive, pure almost without exception, while the coloured forms show various phenomena of dominance. Both found heterozygous colour-types. He then searches for something that looks like a contradiction. Of this there is no lack in the works of Johann von Fischer (11)—an authority of a very different character—whom he quotes in the following few words:

> "In both rats and mice von Fischer says that piebald rats crossed with albino varieties of their species, give piebald young if the father only is piebald, white young if the mother only is piebald."

But this is doing small justice to the completeness of Johann von Fischer's statement, which is indeed a proposition of much more amazing import.

That investigator in fact began by a study of the cross between the albino Ferret and the Polecat, as a means of testing whether they were two species or merely varieties. The cross, he found, was in colour and form a blend of the parental types. Therefore, he declares, the Ferret and the

* The various "contradictions" which Professor Weldon suggests exist between Crampe, von Guaita and Colladon can almost certainly be explained by this circumstance. For Professor Weldon "wild-coloured" mice, however produced, are "wild-coloured" mice and no more (see Introduction).

Polecat are two distinct species, because, "as everybody ought to know,"

"*The result of a cross between albino and normal [of one species] is always a constant one, namely an offspring like the father at least in colour* *,"

whereas in *crosses* (between species) this is *not* the case.

And again, after reciting that the Ferret-Polecat crosses gave intermediates, he states:

"But all this is *not* the case in crosses between albinos and normal animals within the species, in which always and without any exception the young resemble the father in colour †."

These are admirable illustrations of what is meant by a "*universal*" proposition. But von Fischer doesn't stop here. He proceeds to give a collection of evidence in proof of this truth which he says "ought to be known to every-one." He has observed the fact in regard to albino mole, albino shrew (*Sorex araneus*), melanic squirrel (*Sciurus vulgaris*), albino ground-squirrel (*Hypudaeus terrestris*), albino hamster, albino rats, albino mice, piebald (grey-and-white or black-and-white) mice and rats, partially albino sparrow, and we are even presented with two cases in Man. No single exception was known to von Fischer ‡.

* "Das Resultat einer Kreuzung zwischen Albino- und Normal-form ist stets, also, constant, ein dem Vater mindestens in der Färbung gleiches Junge." This law is predicated for the case in which both parents belong to the same species.

† "Dieses Alles ist aber *nie* der Fall bei Kreuzungen unter Leucismen und normalen Thieren innerhalb der Species, bei denen *stets und ohne jede Ausnahme die Jungen in Färbung dem Vater gleichen.*"

‡ He even withdraws two cases of his own previously published, in which grey and albino mice were alleged to have given mixtures, saying that this result must have been due to the broods having been accidentally mixed by the servants in his absence.

In his subsequent paper von Fischer declares that from matings of rats in which the mothers were grey and the fathers albino he bred 2017 pure albinos; and from albino mothers and grey fathers 3830 normal greys. "Not a single individual varied in any respect, or was in any way intermediate."

With piebalds the same result is asserted, save that certain melanic forms appeared. Finally von Fischer repeats his laws already reached, giving them now in this form: *that if the offspring of a cross show only the colour of the father, then the parents are varieties of one species; but if the colour of the offspring be intermediate or different from that of the father, then the parents belong to distinct species.*

The reader may have already gathered that we have here that bane of the advocate—the witness who proves too much. But why does Professor Weldon confine von Fischer to the few modest words recited above? That author has—so far as colour is concerned—a complete law of heredity supported by copious "observations." Why go further?

Professor Weldon "brings forth these strong reasons" of the rats and mice with the introductory sentence:

> "Examples might easily be multiplied, but as before, I have chosen rather to cite a few cases which rest on excellent authority, than to quote examples which may be doubted. I would only add one case among animals, in which the evidence concerning the inheritance of colour is affected by the ancestry of the varieties used."

So once again Professor Weldon suggests that his laws of ancestry will explain even the discrepancies between von Fischer on the one hand and Crampe and von Guaita on the other but he does not tell us how he proposes to apply them.

In the cross between the albino and the grey von Fischer tells us that both colours appear in the offspring, but always, without exception or variation, that of the father only, in 5847 individuals.

Surely, the law of ancestry, if he had a moment's confidence in it, might rather have warned Professor Weldon that von Fischer's results were wrong somewhere, of which there cannot be any serious doubt. The precise source of error is not easy to specify, but probably carelessness and strong preconception of the expected result were largely responsible, though von Fischer says he did all the recording most carefully himself.

Such then is the evidence resting "on excellent authority": may we some day be privileged to see the "examples which may be doubted"?

The case of mice, invoked by Professor Weldon, has also been referred to in our Report. Its extraordinary value as illustrating Mendel's principles and the beautiful way in which that case may lead on to extensions of those principles are also there set forth (see the present Introduction, p. 25). Most if not all of such "conflicting" evidence can be reconciled by the steady application of the Mendelian principle that the progeny will be constant when—and only when*—*similar* gametes meet in fertilisation, apart from any question of the characters of the parent which produces those gametes.

* Excluding "false hybridisations."

V. Professor Weldon's quotations from Laxton.

In support of his conclusions Professor Weldon adduces two passages from Laxton, some of whose testimony we have just considered. This further evidence of Laxton is so important that I reproduce it in full. The first passage, published in 1866, is as follows :—

"The results of experiments in crossing the Pea tend to show that the colour of the immediate offspring or second generation sometimes follows that of the female parent, is sometimes intermediate between that and the male parent, and is sometimes distinct from both; and although at times it partakes of the colour of the male, it has not been ascertained by the experimenter ever to follow the exact colour of the male parent*. In shape, the seed frequently has an intermediate character, but as often follows that of either parent. In the second generation, in a single pod, the result of a cross of Peas different in shape and colour, the seeds are sometimes all intermediate, sometimes represent either or both parents in shape or colour, and sometimes both colours and characters, with their intermediates, appear. The results also seem to show that the third generation or the immediate offspring of a cross, frequently varies from its parents in a limited manner—usually in one direction only, but that the fourth generation produces numerous and wider variations†; the seed often reverting partly to the colour and character of its ancestors of the first generation, partly partaking of the various intermediate colours and characters, and partly sporting quite away from any of its ancestry."

* This is of course on account of the maternal seed characters. Unless the coat-characters are treated separately from the cotyledon-characters Laxton's description is very accurate. Both this and the statements respecting the "shape" of the seeds, a term which as used by Laxton means much more than merely "wrinkled" and "smooth," are recognizably true as general statements.

† Separation of hypallelomorphs.

Here Professor Weldon's quotation ceases. It is unfortunate he did not read on into the very next sentence with which the paragraph concludes :—

"These sports appear to become fixed and permanent in the next and succeeding generations; and the tendency to revert and sport thenceforth seems to become checked if not absolutely stopped*."

Now if Professor Weldon instead of leaving off on the word "ancestry" had noticed this passage, I think his article would never have been written.

Laxton proceeds :—

"The experiments also tend to show that the height of the plant is singularly influenced by crossing; a cross between two dwarf peas, commonly producing some dwarf and some tall [? in the second generation]; but on the other hand, a cross between two tall peas does not exhibit a tendency to diminution in height.

"No perceptible difference appears to result from reversing the parents; the influence of the pollen of each parent at the climax or fourth generation producing similar results†."

The significance of this latter testimony I will presently discuss.

Professor Weldon next appeals to a later paper of Laxton's published in 1890. From it he quotes this passage :

"By means, however, of cross-fertilisation alone, and unless it be followed by careful and continuous selection, the labours of the cross-breeder, instead of benefiting the gardener, may lead to utter confusion,"

* The combinations being exhausted. Perhaps Professor Weldon thought his authority was here lapsing into palpable nonsense!

† Laxton constantly refers to this conception of the "climax" of—as we now perceive—analytical variation and recombination. Many citations could be given respecting his views on this "climax" (cp. p. 167).

Here again the reader would have gained had Professor Weldon, instead of leaving off at the comma, gone on to the end of the paragraph, which proceeds thus :—

"because, as I have previously stated, the Pea under ordinary conditions is much given to sporting and reversion, for when two dissimilar old or fixed varieties have been cross-fertilised, three or four generations at least must, under the most favourable circumstances, elapse before the progeny will become fixed or settled; and from one such cross I have no doubt that, by sowing every individual Pea produced during the three or four generations, hundreds of different varieties may be obtained; but as might be expected, I have found that where the two varieties desired to be intercrossed are unfixed, confusion will become confounded*, and the variations continue through many generations, the number at length being utterly incalculable."

Professor Weldon declares that Laxton's "experience was altogether different from that of Mendel." The reader will bear in mind that when Laxton speaks of fixing a variety he is not thinking particularly of seed-characters, but of all the complex characters, fertility, size, flavour, season of maturity, hardiness, etc., which go to make a serviceable pea. Considered carefully, Laxton's testimony is so closely in accord with Mendelian expectation that I can imagine no chance description in non-Mendelian language more accurately stating the phenomena.

Here we are told in unmistakable terms the breaking up of the original combination of characters on crossing, their re-arrangement, that at the fourth or fifth generation the possibilities of sporting [sub-division of compound allelomorphs and re-combinations of them ?] are exhausted, that there are then definite forms which if selected are

* Further subdivision and recombination of hypallelomorphs.

thenceforth fixed [produced by union of similar gametes?] that it takes longer to select some forms [dominants?] than others [recessives?], that there may be "mule" forms* or forms which cannot be fixed at all† [produced by union of dissimilar gametes?].

But Laxton tells us more than this. He shows us that numbers of varieties may be obtained—hundreds—"incalculable numbers." Here too if Professor Weldon had followed Mendel with even moderate care he would have found the secret. For in dealing with the crosses of *Phaseolus* Mendel clearly forecasts the conception of *compound characters themselves again consisting of definite units*, all of which may be separated and re-combined in the possible combinations, laying for us the foundation of the new science of Analytical Biology.

How did Professor Weldon, after reading Mendel, fail to perceive these principles permeating Laxton's facts? Laxton must have seen the very things that Mendel saw, and had he with his other gifts combined that penetration which detects a great principle hidden in the thin mist of "exceptions," we should have been able to claim for him that honour which must ever be Mendel's in the history of discovery.

When Laxton speaks of selection and the need for it, he means, what the raiser of new varieties almost always means, the selection of *definite* forms, not impalpable fluctuations. When he says that without selection there will be utter confusion, he means—to use Mendelian terms

* For instance the *talls* produced by crossing *dwarfs* are such "mules." Tschermak found in certain cases distinct increase in height in such a case, though not always (p. 531).

† "The remarkably fine but unfixable pea *Evolution*." Laxton, p. 37.

—that the plant which shows the desired combination of characters must be chosen and bred from, and that if this be not done the grower will have endless combinations mixed together in his stock. If however such a selection be made in the fourth or fifth generation the breeder may very possibly have got a fixed form—namely, one that will breed true*. On the other hand he may light on one that does not breed true, and in the latter case it may be that the particular type he has chosen is not represented in the gametes and will *never* breed true, though selected to the end of time. Of all this Mendel has given us the simple and final account.

At Messrs Sutton and Sons, to whom I am most grateful for unlimited opportunities of study, I have seen exactly such a case as this. For many years Messrs Sutton have been engaged in developing new strains of the Chinese Primrose (*Primula sinensis*, hort.). Some thirty thoroughly distinct and striking varieties (not counting the *Stellata* or "Star" section) have already been produced which breed true or very nearly so. In 1899 Messrs Sutton called my attention to a strain known as "Giant Lavender," a particularly fine form with pale magenta or lavender flowers, telling me that it had never become fixed. On examination it appeared that self-fertilised seed saved from this variety gave some magenta-reds, some lavenders, and some which are white on opening but tinge with very faint pink as the flower matures.

On counting these three forms in two successive years the following figures appeared. Two separately bred batches raised from "Giant Lavender" were counted in each year.

* Apart from fresh original variations, and perhaps in some cases imperfect homozygosis of some hypallelomorphs.

	Magenta red	Lavender	White faintly tinged
1901 1st batch	19	27	14
" 2nd "	9	20	9
1902 1st "	12	23	11
" 2nd "	14	26	11
	54	96	45

The numbers 54 : 96 : 45 approach the ratio 1 : 2 : 1 so nearly that there can be no doubt we have here a simple case of Mendelian laws, operating without definite dominance, but rather with blending.

When Laxton speaks of the "remarkably fine but unfixable pea *Evolution*" we now know for the first time exactly what the phenomenon meant. It, like the "Giant Lavender," was a "mule" form, not represented by germ-cells, and in each year arose by "self-crossing."

This is only one case among many similar ones seen in the Chinese Primrose. In others there is no doubt that more complex factors are at work, the subdivision of compound characters, and so on. The history of the "Giant Lavender" goes back many years and is not known with sufficient precision for our purposes, but like all these forms it originated from crossings among the old simple colour varieties of *sinensis*.

VI. The argument built on exceptions.

So much for the enormous advance that the Mendelian principles already permit us to make. But what does Professor Weldon offer to substitute for all this? Nothing.

Professor Weldon suggests that a study of ancestry will help us. Having recited Tschermak's exceptions and the great irregularities seen in the *Telephone* group, he writes :

"Taking these results together with Laxton's statements, and with the evidence afforded by the *Telephone* group of hybrids, I think we can only conclude that segregation of seed-characters is not of universal occurrence among cross-bred peas, and that when it does occur, it may or may not follow Mendel's law."

Premising that when pure types are used the exceptions form but a small part of the whole, and that any supposed absence of "segregation" may have been *variation*, this statement is perfectly sound. He proceeds :—

"The law of segregation, like the law of dominance, appears therefore to hold only for races of *particular ancestry* [my italics]. In special cases, other formulae expressing segregation have been offered, especially by De Vries and by Tschermak for other plants, but these seem as little likely to prove generally valid as Mendel's formula itself.

"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; while the contradictory results obtained by those who have observed the offspring of parents identical in certain characters show clearly enough that not only the parents themselves, but their race, that is their ancestry, must be taken into account before the result of pairing them can be predicted."

In this passage the Mendelian view is none too precisely represented. I should rather have said that it was from Mendel, first of all men, that we have learnt *not* to regard the effects produced on offspring "as due to the existence in the parent of particular structural characters." We have come rather to disregard the particular structure of the parent except in so far as it may give us a guide as to the nature of its gametes.

This indication, if taken in the positive sense—as was sufficiently shown in considering the significance of the "mule" form or "hybrid-character"—we now know may be absolutely worthless, and in any unfamiliar case is very likely to be so. Mendel has proved that the inheritance from individuals of *identical ancestry* may be entirely different: that from identical ancestry, without new variation, may be produced three kinds of individuals (in respect of each pair of characters), namely, individuals capable of transmitting one type, or another type, or both: moreover that the statistical relations of these three classes of individuals to each other will in a great number of cases be a definite one: and of all this he shows a complete account.

Professor Weldon cannot deal with any part of this phenomenon. He does little more than allude to it in passing and point out exceptional cases. These he suggests a study of ancestry will explain.

As a matter of fact a study of ancestry will give little guide—perhaps none—even as to the probability of the phenomenon of dominance of a character, none as to the probability of normal "purity" of germ-cells. Still less will it help to account for fluctuations in dominance, or irregularities in "purity."

Ancestry and Dominance.

In a series of astonishing paragraphs (pp. 241–2) Professor Weldon rises by gradual steps, from the exceptional facts regarding occasional dominance of green colour in *Telephone* to suggest that the *whole phenomenon of dominance may be* *attributable to ancestry*, and that in fact one character has no natural dominance over another, apart from what has been created by selection of ancestry. This piece of reasoning, one of the most remarkable examples of special pleading to be met with in scientific literature, must be read as a whole. I reproduce it entire, that the reader may appreciate this curious effort. The remarks between round parenthetical marks are Professor Weldon's, those between crotchets are mine.

"Mendel treats such characters as yellowness of cotyledons and the like as if the condition of the character in two given parents determined its condition in all their subsequent offspring*. Now it is well known to breeders, and is clearly shown in a number of cases by Galton and Pearson, that the condition of an animal does not as a rule depend upon the condition of any one pair of ancestors alone, but in varying degrees upon the condition of all its ancestors in every past generation, the condition in each of the half-dozen nearest generations having a quite sensible effect. Mendel does not take the effect of differences of ancestry into account, but considers that any yellow-seeded pea, crossed with any green-seeded pea, will behave in a certain definite way, whatever the ancestry of the green and yellow peas may have been. (He does not say this in words, but his attempt to treat his results as generally true of the characters observed is unintelligible unless this hypothesis be assumed.) The experiments afford no evidence which can be held to justify this hypothesis. His observations on cotyledon colour, for example, are based upon 58 cross-fertilised flowers, all of which were borne upon ten plants; and we are not even told whether these ten plants included individuals from more than two races.

"The many thousands of individuals raised from these ten

* Mendel, on the contrary, disregards the "condition of the character" in the parent altogether; but is solely concerned with the nature of the characters of the *gametes*.

plants afford an admirable illustration of the effect produced by crossing a few pairs of plants of known ancestry; but while they show this perhaps better than any similar experiment, they do not afford the data necessary for a statement as to the behaviour of yellow-seeded peas in general, whatever their ancestry, when crossed with green-seeded peas of any ancestry. [Mendel of course makes no such statement.]

"When this is remembered, the importance of the exceptions to dominance of yellow cotyledon-colour, or of smooth and rounded shape of seeds, observed by Tschermak, is much increased; because although they form a small percentage of his whole result, they form a very large percentage of the results obtained with peas of certain races. [Certainly.] The fact that *Telephone* behaved in crossing on the whole like a green-seeded race of exceptional dominance shows that something other than the mere character of the parental generation operated in this case. Thus in eight out of 27 seeds from the yellow *Pois d'Auvergne* ♀ × *Telephone* ♂ the cotyledons were yellow with green patches; the reciprocal cross gave two green and one yellow-and-green seed out of the whole ten obtained; and the cross *Telephone* ♀ × (yellow-seeded) *Buchsbaum** ♂ gave on one occasion two green and four yellow seeds.

"So the cross *Couturier* (orange-yellow) ♀ × the green-seeded *Express* ♂ gave a number of seeds intermediate in colour. (It is not clear from Tschermak's paper whether *all* the seeds were of this colour, but certainly some of them were.) The green *Plein le Panier* [*Fillbasket*] ♀ × *Couturier* ♂ in three crosses always gave either seeds of colour intermediate between green and yellow, or some yellow and some green seeds in the same pod. The cross reciprocal to this was not made; but *Express* ♀ × *Couturier* ♂ gave 22 seeds of which four were yellowish green†.

"These facts show *first* that Mendel's law of dominance conspicuously fails for crosses between certain races, while it

* Regarding this "exception" see p. 146.

† See p. 148.

appears to hold for others; and *secondly* that the intensity of a character in one generation of a race is no trustworthy measure of its dominance in hybrids. The obvious suggestion is that the behaviour of an individual when crossed depends largely upon the characters of its ancestors*. When it is remembered that peas are normally self-fertilised, and that more than one named variety may be selected out of the seeds of a single hybrid pod, it is seen to be probable that Mendel worked with a very definite combination of ancestral characters, and had no proper basis for generalisation about yellow and green peas of any ancestry" [which he never made].

Let us pause a moment before proceeding to the climax. Let the reader note we have been told of *two* groups of cases in which dominance of yellow failed or was irregular. (Why are not Gärtner's and Seton's "exceptions" referred to here?) In one of these groups *Couturier* was always one parent, either father or mother, and were it not for Tschermak's own obvious hesitation in regard to his own exceptions (see p. 148), I would gladly believe that *Couturier*—a form I do not know—may be an exceptional variety. *How* Professor Weldon proposes to explain its peculiarities by reference to ancestry he omits to tell us. The *Buchsbaum* case is already disposed of, for on Tschermak's showing, it is an unstable form.

Happily, thanks to Professor Weldon, we know rather more of the third case, that of *Telephone*, which, whether as father or mother, was frequently found by Tschermak to give either green, greenish, or patchwork-seeds when crossed with yellow varieties. It behaves, in short, "like a green-seeded pea of exceptional dominance," as we are now told. For this dominant quality of *Telephone's* greenness we are asked to account *by appeal to its ancestry*. May we not

* Where was that "logician," the "consulting-partner," when this piece of reasoning passed the firm?

expect, then, this *Telephone* to be—if not a pure-bred green pea from time immemorial—at least as pure-bred as other green peas which do *not* exhibit dominance of green at all? Now, what is *Telephone*? Do not let us ask too much. Ancestry takes a lot of proving. We would not reject him "*parce qu'il n'avait que soixante & onze quartiers, & que le reste de son arbre généalogique avait été perdu par l'injure du tems.*"

But with stupefaction we learn from Professor Weldon himself that *Telephone* is the very variety which he takes *as his type of a permanent and incorrigible mongrel*, a character it thoroughly deserves.

From *Telephone* he made his colour scale! Tschermak declares the cotyledons to be "yellowish or whitish green, often entirely bright yellow*." So little is it a thorough-bred green pea, that it cannot always keep its own self-fertilised offspring green. Not only is this pea a parti-coloured mongrel, but Professor Weldon himself quotes Culverwell that as late as 1882 both *Telegraph* and *Telephone* "will always come from one sort, more especially from the green variety"; and again regarding a supposed good sample of *Telegraph* that "Strange to say, although the peas were taken from one lot, those sown in January produced a great proportion of the light variety known as *Telephone*. These were of every shade of light green up to white, and could have been shown for either variety," *Gard. Chron.* 1882 (2), p. 150. This is the variety whose green, it is suggested, partially "dominates" over the yellow of *Pois d'Auvergne*, a yellow variety which has a clear lineage of about a century, and probably more. If, therefore, the facts regarding *Telephone* have any bearing on the signi-

* "*Speichergewebe gelblich—oder weisslich—grün, manchmal auch vollständig hellgelb.*" Tschermak (36), p. 480.

ficance of ancestry, they point the opposite way from that in which Professor Weldon desires to proceed.

In view of the evidence, the conclusion is forced upon me that the suggestion that "ancestry" may explain the facts regarding *Telephone* has no meaning behind it, but is merely a verbal obstacle. Two words more on *Telephone.* On p. 147 I ventured to hint that if we try to understand the nature of the appearance of green in the offspring of *Telephone* bred with yellow varieties, we are more likely to do so by comparing the facts with those of false hybridisation than with fluctuations in dominance. In this connection I would call the reader's attention to a point Professor Weldon misses, that Tschermak *also got yellowish-green seeds from Fillbasket (green) crossed with Telephone.* I suggest therefore that *Telephone's* allelomorphs may be in part transmitted to its offspring in a state which needs no union with any corresponding allelomorph of the other gamete, just as may the allelomorphs of "false hybrids." It would be quite out of place here to pursue this reasoning, but the reader acquainted with special phenomena of heredity will probably be able fruitfully to extend it. It will be remembered that we have already seen the further fact that the behaviour of *Telephone* in respect to seed-shape was also peculiar (see p. 152).

Whatever the future may decide on this interesting question it is evident that with *Telephone* (and possibly *Buchsbaum*) we are encountering a *specific* phenomenon, which calls for specific elucidation and not a case simply comparable with or contradicting the evidence of dominance in general.

In this excursion we have seen something more of the "exceptions." Many have fallen, but some still stand, though even as to part of the remainder Tschermak entertains some doubts, and, it will be remembered, cautions his reader that of his exceptions some may be self-fertilisations, and some did not germinate*. Truly a slender basis to carry the coming structure!

But Professor Weldon cannot be warned. He told us the "law of dominance conspicuously fails for crosses between certain races." Thence the start. I venture to give the steps in this impetuous argument. There are exceptions†—a fair number if we count the bad ones—there may be more—must be more—*are* more—no doubt many more: so to the brink. Then the bold leap: may there not be as many cases one way as the other? We have not tried half the sorts of Peas yet. There is still hope. True we know dominance of many characters in some hundreds of crosses, using some twenty varieties—not to speak of other plants and animals—but we *do* know some exceptions, of which a few are still good. So dominance

* In his latest publication on this subject, the notes to the edition of Mendel in Ostwald's *Klassiker* (pp. 60—61), Tschermak, who has seen more true exceptions than any other observer, thus refers to them. As to dominance:—"*Immerhin kommen vereinzelt auch zweifellose Fälle von Merkmalmischung, d. h. Uebergangsformen zwischen gelber und grüner Farbe, runder und runzeliger Form vor, die sich in weiteren Generationen wie dominantmerkmalige Mischlinge verhalten.*" As to purity of the extracted recessives:—*Ganz vereinzelt scheinen Ausnahmsfälle vorzukommen.*"

Küster (22) also in a recent note on Mendelism points out, with reason, that the number of "exceptions" to dominance that we shall find, depends simply on the stringency with which the supposed "law" is drawn. The same writer remarks further that Mendel makes no such rigid definition of dominance as his followers have done.

† If the "logician-consulting-partner" will successfully apply this *Fallacia acervalis*, the "method of the vanishing heap," to dominant peas, he will need considerable leisure.

may yet be all a myth, built up out of the petty facts those purblind experimenters chanced to gather. Let us take wider views. Let us look at fields more propitious—more what we would have them be! Let us turn to eye-colour: at least there is no dominance in that. Thus Professor Weldon, telling us that Mendel "had no proper basis for generalisation about yellow and green peas of any ancestry," proceeds to this lamentable passage:—

"Now in such a case of alternative inheritance as that of human eye-colour, it has been shown that a number of pairs of parents, one of whom has dark and the other blue eyes, will produce offspring of which nearly one half are dark-eyed, nearly one half are blue-eyed, a small but sensible percentage being children with mosaic eyes, the iris being a patch-work of lighter and darker portions. But the dark-eyed and light-eyed children are not equally distributed among all families; and it would almost certainly be possible, by selecting cases of marriage between men and women of appropriate ancestry, to demonstrate for their families a law of dominance of dark over light eye-colour, or of light over dark. Such a law might be as valid for the families of selected ancestry as Mendel's laws are for his peas and for other peas of probably similar ancestral history, but it would fail when applied to dark and light-eyed parents in general,—that is, to parents of any ancestry who happen to possess eyes of given colour."

The suggestion amounts to this: that because there are exceptions to dominance in peas; and because by some stupendous coincidence, or still more amazing incompetence, a bungler might have thought he found dominance of one eye-colour whereas really there was none*; therefore

* I have no doubt there is no universal dominance in eye-colour. Is it *quite* certain there is no dominance at all? I have searched the works of Galton and Pearson relating to this subject without finding a clear proof. If there is in them material for this decision

Professor Weldon is at liberty to suggest there is a fair chance that Mendel and all who have followed him have either been the victims of this preposterous coincidence not once, but again and again; or else persisted in the same egregious and perfectly gratuitous blunder. Professor Weldon is skilled in the Calculus of Chance: will he compute the probabilities in favour of his hypothesis?

Ancestry and purity of germ-cells.

To what extent ancestry is likely to elucidate dominance we have now seen. We will briefly consider how laws derived from ancestry stand in regard to segregation of characters among the gametes.

For Professor Weldon suggests that his view of ancestry will explain the facts not only in regard to dominance and its fluctuations but in regard to the purity of the germ-cells. He does not apply this suggestion in detail, for its error would be immediately exposed. In every strictly Mendelian case the *ancestry* of the pure extracted recessives or dominants, arising from the breeding of first crosses, is identical with that of the impure dominants [or impure recessives in cases where they exist]. Yet the posterity of each is wholly different. The pure extracted forms, in these simplest cases, are no more likely to produce the form with which they have been crossed than was their pure grandparent; while the impure forms break up again into both grand-parental forms.

Ancestry does not touch these facts in the least. They

I may perhaps be pardoned for failing to discover it, since the tabulations are not prepared with this point in view. Reference to the original records would soon clear up the point.

and others like them have been a stumbling-block to all naturalists. Of such paradoxical phenomena Mendel now gives us the complete and final account. Will Professor Weldon indicate how he proposes to regard them?

Let me here call the reader's particular attention to that section of Mendel's experiments to which Professor Weldon does not so much as allude. Not only did Mendel study the results of allowing his cross-breds (DR's) to fertilise themselves, giving the memorable ratio

$$1\,DD : 2\,DR : 1\,RR,$$

but he fertilised those cross-breds (DR's) both with the pure dominant (D) and with the pure recessive (R) varieties reciprocally, obtaining in the former case the ratio

$$1\,DD : 1\,DR$$

and in the latter the ratio

$$1\,DR : 1\,RR.$$

The DD group and the RR group thus produced giving on self-fertilisation pure D offspring and pure R offspring respectively, while the DR groups gave again

$$1\,DD : 2\,DR : 1\,RR.$$

How does Professor Weldon propose to deal with these results, and by what reasoning can he suggest that considerations of ancestry are to be applied to them? If I may venture to suggest what was in Mendel's mind when he applied this further test to his principles it was perhaps some such considerations as the following. Knowing that the cross-breds on self-fertilisation give

$$1\,DD : 2\,DR : 1\,RR$$

three explanations are possible:

(*a*) These cross-breds may produce pure *D* germs of both sexes and pure *R* germs of both sexes on an average in equal numbers.

(*b*) *Either* the female, *or* the male, gametes may be *alone* differentiated according to the allelomorphs, into pure *D*'s, pure *R*'s, and crosses *DR* or *RD*, the gametes of the other sex being homogeneous and neutral in regard to those allelomorphs.

(*c*) There may be some neutralisation or cancelling between characters in *fertilisation* occurring in such a way that the well-known ratios resulted. The absence of and inability to transmit the *D* character in the *RR*'s, for instance, might have been due not to the original purity of the germs constituting them, but to some condition incidental to or connected with fertilisation.

It is clear that Mendel realized (*b*) as a possibility, for he says *DR* was fertilised with the pure forms to test the composition of its egg-cells, but the reciprocal crosses were made to test the composition of the pollen of the hybrids. Readers familiar with the literature will know that both Gärtner and Wichura had in many instances shown that the offspring of crosses in the form $(a \times b)$ ♀ × c ♂ were less variable than those of crosses in the form a ♀ × $(b \times c)$ ♂, &c. This important fact in many cases is observed, and points to differentiation of characters occurring frequently among the male gametes when it does not occur or is much less marked among the maternal gametes. Mendel of course knew this, and proceeded to test for such a possibility, finding by the result that differentiation was the same in the gametes of both sexes*.

* See Wichura (46), pp. 55–6.

Of hypotheses (*b*) and (*c*) the results of recrossing with the two pure forms dispose; and we can suggest no hypothesis but (*a*) which gives an acceptable account of the facts.

It is the purity of the "extracted" recessives and the "extracted" dominants—primarily the former, as being easier to recognize—that constitutes the real proof of the validity of Mendel's principle.

Using this principle we reach immediately results of the most far-reaching character. These theoretical deductions cannot be further treated here—but of the practical use of the principle a word may be said. Where-ever there is marked dominance of one character the breeder can at once get an indication of the amount of trouble he will have in getting his cross-bred true to either dominant or recessive character. He can only thus forecast the future of the race in regard to each such pair of characters taken severally, but this is an immeasurable advance on anything we knew before. More than this, it is certain that in some cases he will be able to detect the "mule" or heterozygous forms by the statistical frequency of their occurrence or by their structure, especially when dominance is absent, and sometimes even in cases where there is distinct dominance. With peas, the practical seedsman cares, as it happens, little or nothing for those simple characters of seed-structure, &c. that Mendel dealt with. He is concerned with size, fertility, flavour, and numerous similar characters. It is to these that Laxton (invoked by Professor Weldon) primarily refers, when he speaks of the elaborate selections which are needed to fix his novelties.

We may now point tentatively to the way in which some even of these complex cases may be elucidated by an extension of Mendel's principle, though we cannot forget that there are other undetected factors at work.

The value of the appeal to Ancestry.

But it may be said that Professor Weldon's appeal to ancestry calls for more specific treatment. When he suggests ancestry as "one great reason" for the different properties displayed by different races or individuals, and as providing an account of other special phenomena of heredity, he is perhaps not to be taken to mean any definite ancestry, known or hypothetical. He may, in fact, be using the term "ancestry" merely as a brief equivalent signifying the previous history of the race or individual in question. But if such a plea be put forward, the real utility and value of the appeal to ancestry is even less evident than before.

Ancestry, as used in the method of Galton and Pearson, means a definite thing. The whole merit of that method lies in the fact that by it a definite accord could be proved to exist between the observed characters and behaviour of specified descendants and the ascertained composition of their pedigree. Professor Weldon in now attributing the observed peculiarities of *Telephone* &c. to conjectural peculiarities of pedigree—if this be his meaning—renounces all that had positive value in the reference to ancestry. His is simply an appeal to ignorance. The introduction of the word "ancestry" in this sense contributes nothing. The suggestion that ancestry might explain peculiarities means no more than "we do not know how peculiarities are to be explained." So Professor Weldon's phrase "peas of probably similar ancestral history *" means "peas probably

* See above, p. 192.

similar"; when he speaks of Mendel having obtained his results with "a few pairs of plants of known ancestry*," he means "a few pairs of known plants" and no more; when he writes that "the law of segregation, like the law of dominance appears to hold only for races of particular ancestry†," *the statement loses nothing if we write simply* "for particular races." We all know—the Mendelian, best of all—that particular races and particular individuals may, even though indistinguishable by any other test, exhibit peculiarities in heredity.

But though on analysis those introductions of the word "ancestry" are found to add nothing, yet we can feel that as used by Professor Weldon they are intended to mean a great deal. Though the appeal may be confessedly to ignorance, the suggestion is implied that if we did know the pedigrees of these various forms we should then have some real light on their present structure or their present behaviour in breeding. Unfortunately there is not the smallest ground for even this hope.

As Professor Weldon himself tells us‡, conclusions from pedigree must be based on the conditions of the several ancestors; and even more categorically (p. 244), "*The degree to which a parental character affects offspring depends not only upon its development in the individual parent, but on its degree of development in the ancestors of that parent.*" [My italics.] Having rehearsed this profession of an older faith Professor Weldon proceeds to stultify it in his very next paragraph. For there he once again reminds us that *Telephone*, the mongrel pea of recent origin, which does not breed true to seed characters, has yet manifested the peculiar power of stamping the recessive characters on its cross-bred

* See above, p. 187. † See above, p. 184.

‡ See above, p. 186.

offspring, though pure and stable varieties that have exhibited the same characters in a high degree for generations have *not* that power. As we now know, the presence or absence of a character in a progenitor *may* be no indication whatever as to the probable presence of the character in the offspring; for the characters of the latter depend on gametic and not on zygotic differentiation.

The problem is of a different order of complexity from that which Professor Weldon suggests, and facts like these justify the affirmation that if we could at this moment bring together the whole series of individuals forming the pedigree of *Telephone*, or of any other plant or animal known to be aberrant as regards heredity, we should have no more knowledge of the nature of these aberrations; no more prescience of the moment at which they would begin, or of their probable modes of manifestation; no more criterion in fact as to the behaviour such an individual would exhibit in crossing*, or solid ground from which to forecast its posterity, than we have already. We should learn then—what we know already—that at some particular point of time its peculiar constitution was created, and that its peculiar properties then manifested themselves: how or why this came about, we should no more comprehend with the full ancestral series before us, than we can in ignorance of the ancestry. Some cross-breds follow Mendelian segregation; others do not. In some, palpable dominance appears; in others it is absent.

If there were no ancestry, there would be no posterity. But to answer the question *why* certain of the posterity depart from the rule which others follow, we must know, not the ancestry, but how it came about *either* that at a

* Beyond an indication as to the homogeneity or "purity" of its gametes at a given time.

certain moment a certain gamete divided from its fellows in a special and unwonted fashion; *or*, though the words are in part tautological, the reason why the union of two particular gametes in fertilisation took place in such a way that gametes having new specific properties resulted*. No one yet knows how to use the facts of ancestry for the elucidation of these questions, or how to get from them a truth more precise than that contained in the statement that a diversity of specific consequences (in heredity) may follow an apparently single specific disturbance. Rarely even can we see so much. The appeal to ancestry, as introduced by Professor Weldon, masks the difficulty he dare not face.

In other words, it is the *cause of variation* we are here seeking. To attack that problem no one has yet shown the way. Knowledge of a different order is wanted for that task; and a compilation of ancestry, valuable as the exercise may be, does not provide that particular kind of knowledge.

Of course when once we have discovered by experiment that—say, *Telephone*—manifests a peculiar behaviour in heredity, we can perhaps make certain forecasts regarding it with fair correctness; but that any given race or individual will behave in such a way, is a fact not deducible from its ancestry, for the simple reason that organisms of identical ancestry may behave in wholly distinct, though often definite, ways.

It is from this hitherto hopeless paradox that Mendel has begun at last to deliver us. The appeal to ancestry is a substitution of darkness for light.

* May there be a connection between the extraordinary fertility and success of the *Telephone* group of peas, and the peculiar frequency of a blended or mosaic condition of their allelomorphs? The conjecture may be wild, but it is not impossible that the two phenomena may be interdependent.

VII. The question of absolute purity of germ-cells.

But let us go back to the cases of defective "purity" and consider how the laws of ancestry stand in regard to them. It appears from the facts almost certain that purity may sometimes be wanting in a character which elsewhere usually manifests it.

Here we approach a question of greater theoretical consequence to the right apprehension of the part borne by Mendelian principles in the physiology of heredity. We have to consider the question whether the purity of the gametes in respect of one or other antagonistic character is or is likely to be in case of *any* given character a *universal* truth? The answer is unquestionably—No—but for reasons in which "ancestry" plays no part*.

Hoping to interest English men of science in the Mendelian discoveries I offered in November 1900 a paper on this subject to "Nature." The article was of some length and exceeded the space that the Editor could grant without delay. I did not see my way to reduce it without injury to clearness, and consequently it was returned to me. At the time our own experiments were not ready for publication and it seemed that all I had to say would probably be common knowledge in the next few weeks, so no further attempt at publication was made.

In that article I discussed this particular question of the absolute purity of the germ-cells, showing how, on the analogy of other bud-variations, it is almost certain that the germ-cells, even in respect to characters normally Mendelian, may on occasion present the same mixture of characters, whether apparently blended or mosaic, which

* This discussion leaves "false hybridism" for separate consideration.

we know so well elsewhere. Such a fact would in nowise diminish the importance of Mendel's discovery. The fact that mosaic peach-nectarines occur is no refutation of the fact that the *total* variation is common. Just as there may be trees with several such mosaic fruits, so there may be units, whether varieties, individual plants, flowers or gonads, or other structural units, bearing mosaic egg-cells or pollen grains. Nothing is more likely or more in accordance with analogy than that by selecting an individual producing germs of blended or mosaic character, a race could be established continuing to produce such germs. Persistence of such blends or mosaics in *asexual* reproduction is well-known to horticulturists; for example "bizarre" carnations, oranges streaked with "blood"-orange character, and many more. In the famous paper of Naudin, who came nearer to the discovery of the Mendelian principle than any other observer, a paper quoted by Professor Weldon, other examples are given. These forms, once obtained, can be multiplied *by division*; and there is no reason why a zygote formed by the union of mosaic or blended germs, once arisen, should not in the cell-divisions by which its gametes are formed, continue to divide in a similar manner and produce germs like those which united to form that zygote. The irregularity, once begun, may continue for an indefinite number of divisions.

I am quite willing to suppose, with Professor Weldon (p. 248), that the pea *Stratagem* may, as he suggests, be such a case. I am even willing to accept provisionally as probable that when two gametes, themselves of mosaic or blended character, meet together in fertilisation, they are more likely to produce gametes of mosaic or blended character than of simply discontinuous character. Among Messrs Sutton's Primulas there are at least two striking cases of "flaked" or "bizarre" unions of bright colours and white which reproduce themselves by seed with fair constancy, though Mendelian purity in respect of these colours is elsewhere common in the varieties (I suspect mosaics of "false hybridism" among allelomorphs in some of these cases). Similarly Galton has shown that though children having one light-eyed and one dark-eyed parent generally have eyes either light or dark, the comparatively rare medium eye-coloured persons when they mate together frequently produce children with medium eye-colour.

In this connection it may be worth while to allude to a point of some practical consequence. We know that when pure dominant—say yellow—is crossed with pure recessive—say green—the dominance of yellow is seen; and we have every reason to believe this rule generally (*not* universally) true for pure varieties of peas. But we notice that in the case of a form like the pea, depending on human selection for its existence, it might be possible in a few years for the races with pure seed characters to be practically supplanted by the "mosaicized" races like the *Telephone* group, if the market found in these latter some specially serviceable quality. In the maincrop peas I suspect this very process is taking place*. After such a

* Another practical point of the same nature arises from the great variability which these peas manifest in plant- as well as seed-characters. Mr Hurst of Burbage tells me that in *e.g. William the First*, a pea very variable in seed-characters also, tall plants may be so common that they have to be rogued out even when the variety is grown for the vegetable market, and that the same is true of several such varieties. It seems by no means improbable that it is by such roguing that the unstable mosaic or blend-form is preserved. In a thoroughly stable variety such as *Ne Plus Ultra* roguing is hardly necessary even for the seed-market.

Mr N. N. Sherwood in his useful account of the origin and races revolution it might be possible for a future experimenter to conclude that *Pisum sativum* was by nature a "mosaicized" species in these respects, though the mosaic character may have arisen once in a seed or two as an exceptional phenomenon. When the same reasoning is extended to wild forms depending on other agencies for selection, some interesting conclusions may be reached.

But in Mendelian cases we are concerned primarily not with the product of gametes of blended character, but with the consequences of the union of gametes already discontinuously dissimilar. The existence of pure Mendelian gametes for given characters is perfectly compatible with the existence of blended or mosaic gametes for similar characters elsewhere, but this principle enables us to form a comprehensive and fruitful conception of the relation of the two phenomena to each other. As I also pointed out, through the imperfection of our method which does not yet permit us to *see* the differentiation among the gametes though we know it exists, we cannot yet as a rule obtain certain proof of the impurity of the gametes (except perhaps in the case of mosaics) as distinct from evidence of imperfect dominance. If however the case be one of a "mule" form, distinct from either parent, and not merely of dominance, there is no *a priori* reason why even this may not be possible; for we should be able to

of peas (*Jour. R. Hort. Soc.* XXII. 1899, p. 254) alludes to the great instability of this class of pea. To Laxton, he says, "we are indebted for a peculiar type of Pea, a round seed with a very slight indent, the first of this class sent out being *William the First*, the object being to get a very early blue-seeded indented Pea of the same earliness as the Sangster type with a blue seed, or in other words with a Wrinkled Pea flavour. This type of Pea is most difficult to keep true on account of the slight taint of the Wrinkled Pea in the breed, which causes it to run back to the Round variety."

distinguish the results of breeding first crosses together into *four* classes: two pure forms, one or more blend or mosaic forms, and "mule" forms. Such a study could as yet only be attempted in simplest cases: for where we are concerned with a compound allelomorph capable of resolution, the combinations of the integral components become so numerous as to make this finer classification practically inapplicable.

But in many cases—perhaps a majority—though by Mendel's statistical method we can perceive the fluctuations in the numbers of the several products of fertilisation, we shall not know whether abnormalities in the distribution of those products are due to a decline in dominance, or to actual impurity of the gametes. We shall have further to consider, as affecting the arithmetical results, the possibility of departure from the rule that each kind of gamete is produced in equal numbers*; also that there may be the familiar difficulties in regard to possible selection and assortative matings among the gametes.

I have now shown how the mosaic and blend-forms are to be regarded in the light of the Mendelian principle. What has Professor Weldon to say in reference to them? His suggestion is definite enough—that a study of ancestry will explain the facts: *how*, we are not told.

In speaking of the need of study of the characters of the *race* he is much nearer the mark, but when he adds "that is their ancestry," he goes wide again. When *Telephone* does not truly divide the antagonistic characters among its germ-cells this fact is in nowise simply traceable to its having originated in a cross—a history it shares with almost all the peas in the market—but to its own peculiar

* In dealing with cases of decomposition or resolution of compound characters this consideration is of highest importance.

nature. In such a case imperfect dominance need not surprise us.

What we need in all these phenomena is a knowledge of the properties of each race, or variety, as we call it in peas. We must, as I have often pleaded, study the properties of each form no otherwise than the chemist does the properties of his substances, and thus only can we hope to work our way through these phenomena. *Ancestry* holds no key to these facts; for the same ancestry is common to own brothers and sisters endowed with dissimilar properties and producing dissimilar posterity. To the knowledge of the properties of each form and the laws which it obeys there are no short cuts. We have no periodic law to guide us. Each case must as yet be separately worked out.

We can scarcely avoid mention of a further category of phenomena that are certain to be adduced in opposition to the general truth of the purity of the extracted forms. It is a fact well known to breeders that a highly-bred stock may, unless selections be continued, "degenerate." This has often been insisted on in regard to peas. I have been told of specific cases by Messrs Sutton and Sons, instances which could be multiplied. Surely, will reply the supporters of the theory of Ancestry, this is simply impurity in the extracted stocks manifesting itself at last. Such a conclusion by no means follows, and the proof that it is inapplicable is obtained from the fact that the "degeneration," or variation as we should rather call it, need not lead to the production of any proximate ancestor of the selected stock at all, but immediately to a new form, or to one much more remote—in the case of some high class peas, *e.g.*, to the form which Mr Sutton describes as "vetch-like," with short pods, and a very few small round seeds, two or three in a pod. Such plants are recognized by their appearance and are rigorously hoed out every year before seeding.

To appreciate the meaning of these facts we must go back to what was said above on the nature of compound characters. We can perceive that, as Mendel showed, the integral characters of the varieties can be dissociated and re-combined in any combination. More than that; certain integral characters can be resolved into further integral components, by *analytical* variations. What is taking place in this process of resolution we cannot surmise, but we may liken the consequences of that process to various phenomena of analysis seen elsewhere. To continue the metaphor we may speak of return to the vetch-like type as a *synthetical* variation: well remembering that we know nothing of any *substance* being subtracted in the former case or added in the latter, and that the phenomenon is more likely to be primarily one of alteration in arrangement than in substance.

A final proof that nothing is to be looked for from an appeal to ancestry is provided by the fact—of which the literature of variation contains numerous illustrations—that such newly synthesised forms, instead of themselves producing a large proportion of the high class variety which may have been their ancestor for a hundred generations, may produce almost nothing but individuals like themselves. A subject fraught with extraordinary interest will be the determination whether by crossing these newly synthesised forms with their parent, or another pure form, we may not succeed in reproducing a great part of the known series of components afresh. The pure parental form, produced, or extracted, by "analytical" breeding, would not in ordinary circumstances be capable of producing the other components from which it has been separated; but by crossing it with the "synthesised" variety it is not impossible that these components would again reappear. If this can be shown to be possible we shall have entirely new light on the nature of variation and stability.

Conclusion.

I trust what I have written has convinced the reader that we are, as was said in opening, at last beginning to move. Professor Weldon declares he has "no wish to belittle the importance of Mendel's achievement"; he desires "simply to call attention to a series of facts which seem to him to suggest fruitful lines of inquiry." In this purpose I venture to assist him, for I am disposed to think that unaided he is—to borrow Horace Walpole's phrase—about as likely to light a fire with a wet dish-clout as to kindle interest in Mendel's discoveries by his tempered appreciation. If I have helped a little in this cause my time has not been wasted.

In these pages I have only touched the edge of that new country which is stretching out before us, whence in ten years' time we shall look back on the present days of our captivity. Soon every science that deals with animals and plants will be teeming with discovery, made possible by Mendel's work. The breeder, whether of plants or of animals, no longer trudging in the old paths of tradition, will be second only to the chemist in resource and in foresight. Each conception of life in which heredity bears a part—and which of them is exempt?—must change before the coming rush of facts.