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 thoroughbred 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 enter-

tains 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 $(a \times b)\ ♀ \times c\ ♂$ were less variable than those of crosses in the form $a\ ♀ \times (b \times c)\ ♂$, &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. Wherever 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. 194.

‡ 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.