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MENDEL'S LAWS OF ALTERNATIVE INHERITANCE IN PEAS.

W. F. R. WELDON

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IF TWO PLANTS, or two animals, of different characters be allowed to breed together, the parental characters may affect the offspring in any one of three ways. In the most usual case, the characters by which the parents differ may appear so intimately blended in the offspring that each young animal or plant appears intermediate in character between its parents, but it is not generally possible for us at present to resolve its body into separate elements, some of which resemble one parent, and some the other. In other cases, however, the body of the young is easily divisible into regions, in some of which the character of one parent is presented in a recognizable and often apparently unaltered state, while the rest of the body presents a similar resemblance to the other parent. In the cases of the third class the body of the offspring may entirely resemble that of one parent, the characters of the other being apparently unrepresented. While it is perfectly possible and indeed probable that the difference between these three forms of inheritance is only one of degree, it is still convenient to discuss them separately.

The work of Galton (No. 13) and Pearson (No. 24) has given us an expression for the effects of *blended* inheritance which seems likely to prove generally applicable, although 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. It is the purpose of this essay to describe some cases of alternative inheritance, which have lately excited attention, and to discuss the contradictory evidence concerning them.

I. — MENDEL'S RESULTS WITH PEAS.

In 1865 Gregor Mendel (No. 21) described the results of crossing various races of the common Pea. He does not waste time in discussing the question whether all his races belong to one "species" or not, but describes the result of crossing any two of them as "hybrid." It is probable, however, that all his races belonged to what is now called *Pisum sativum* to the exclusion of *Pisum arvense*.

The races used differed, no doubt, in many ways: but special attention is paid to seven sets of characters, with regard to each of which it was possible to separate the races into two categories. Thus the shape of the seeds might be round, with only slight and shallow wrinkles on the surface, or irregular and deeply wrinkled. The cotyledons of the seeds might be yellow or green in colour, and so on. The pairs of characters, recognised in this way for each organ or set of organs studied, are distinguished, according to their power of affecting hybrid offspring, into *dominant* and *recessive*. The characters presented by a race are not necessarily all "dominant," or all "recessive"; thus the character of roundness in seeds is dominant, that of wrinkled irregular shape recessive; yellow colour of cotyledons is dominant, and green recessive; but a race of peas may have smooth and rounded seeds with green cotyledons, or yellow cotyledons and wrinkled seeds.

The first general result obtained by Mendel may be stated as follows: *If peas of two races be crossed, the hybrid offspring will exhibit only the dominant characters of the parents; and it will exhibit these without (or almost without) alteration, the recessive characters being altogether absent, or present in so slight a degree that they escape notice.*

This may be called the Law of Dominance, and it at once explains the terms dominant and recessive.

The second result is that: *If the hybrids of the first generation, produced by crossing two races of peas which differ in certain characters, be allowed to fertilize themselves, all possible combinations of the ancestral race-characters will appear in the second generation with equal frequency, and these combinations will obey the Law of*

Dominance, so that characters intermediate between those of the ancestral races will not occur.

From its consequences, this may be called the Law of Segregation.

The significance of these results may most easily be seen by considering an example. It has been said that yellowness of cotyledons is dominant over greenness of cotyledons. That is to say, if a plant from a race with yellow cotyledons and one from a race with green cotyledons be cross-fertilised, the resulting seeds will have yellow cotyledons, no matter which plant be used as the female parent. Mendel chose ten plants, some from a race with green and some from a race with yellow cotyledons, and upon these plants he made 58 crosses, so that the ♀ parent was sometimes of green-seeded, sometimes of yellow-seeded race. The resulting seeds had always yellow cotyledons. From these seeds 258 plants were grown, which produced 8023 seeds; and these seeds had the characters indicated by the law of segregation. The combinations of pure ancestral character, which are here possible, are four; since the gamete of either sex may conceivably be capable of transmitting either “yellowness” or “greenness” of cotyledon; Mendel’s assumption is that every gamete inherits only one of these “alternative” characters, half the gametes of either sex inheriting each character, or the power of transmitting it, so that there may conceivably be the following combinations:

♀	yellow	×	yellow	♂
♀	yellow	×	green	♂
♀	green	×	yellow	♂
♀	green	×	green	♂

But by the law of dominance, if unlike gametes unite, the resultant seed has the dominant character, while if similar gametes unite the resultant seed has naturally the character transmitted by both its constituent gametes. It follows that three of the above combinations give rise to seeds with yellow cotyledons, and only one to green seeds; and if each combination occurs equally often, the chance that a given hybrid seed of the second generation will be yellow is ¾, the chance that it will be green is ¼.

Now, of the 8023 seeds of Mendel’s second generation, 6022 were yellow and 2001 green. Seeds of intermediate colour did not occur. The ratio between either of these numbers and the number of seeds observed is an excellent approximation to that required by Mendel’s law of segregation.* The plants of the first hybrid generation invariably bore seeds of both colours, and as a rule seeds of both colours were

* See below, Table I. p. 7.

associated in the same pod. Pods containing only yellow seeds did occur, pods with green seeds only did not. This is all in accordance with the law of segregation; for the number of peas per pod being from six to nine, the chance of getting a pod with yellow seeds only is from $(¾)^6$ for pods with six seeds to $(¾)^9$ for pods with nine seeds, or from 0.18 to 0.075; so that about 18 per cent. of smaller, and about 8 per cent. of larger pods, should contain only yellow seeds; but the chance of a pod containing even six green and no yellow seeds is only $(¼)^6$ = 1/4096. Assuming that there were some 1500 pods on the plants, it is clear that the absence of pods without yellow seeds is in good accord with Mendel's law of dominance.

The third hybrid generation must, if the foregoing statements are true, be heterogeneous, for the hybrid seeds of the second generation are said to be of three kinds; those formed by the union of two gametes each transmitting only dominant characters, those formed from gametes each transmitting only recessive characters, and those formed from the union of dissimilar gametes. Therefore the offspring of these seeds should also be of three kinds; in the case before us, one kind, produced from yellow seeds, should give rise to yellow-seeded plants, like those of their pure-bred yellow-seeded ancestors; one kind, produced from green seeds, should give rise to apparently pure-bred green-seeded plants; while the third kind, being yellow seeds produced by the union of one gamete with "dominant" and one with "recessive" properties, should give rise to plants identical with the hybrids of the first generation. This result was actually obtained. Those seeds of the second hybrid generation, which had green cotyledons, gave rise to plants which in turn produced only green seeds. From the yellow seeds of the second hybrid generation 519 plants were raised, of which 166 produced only yellow seeds, behaving therefore like pure-bred plants of yellow race, and 353 had both yellow and green seeds, in the proportion of three yellow to one green, as in the first hybrid generation. The observations were continued through six generations; and the descendants of those plants of the second generation which produced only one kind of seed remained throughout apparently pure-bred, producing each its proper kind of seed as regularly as its pure-bred ancestors; the hybrids of every generation behaved exactly like those of the first or second generation. The result of this process is that the percentage of hybrids diminishes in every generation: for suppose each plant in each generation to produce four seeds only, the plants of the first hybrid generation will produce one apparently pure-bred yellow-seeded and one apparently pure-bred green-seeded plant, with two hybrids; in the third generation there will be four apparently pure-bred yellow plants from the apparently pure yellow-seeded plant of the second generation, and two others, one from each hybrid; there will in the same way be six apparently pure green-seeded plants, and four hybrids. Assuming this process to go on, the numbers in successive generations will be:

Generation	Yellow	Hybrid	Green
1		1	
2	1	2	1
3	6	4	6
4	28	8	28
5	120	16	120
6	496	32	496
etc.			

So that the number of apparently pure-bred forms of each kind increases, and in the (n+1)th hybrid generation, the three classes of plants are in the proportions of $2^n - 1 : 2 : 2^n - 1$.

Results closely similar to these were obtained with seven sets of differential characters; namely

1. *The shape of the seed* (round and feebly wrinkled, *dominant*; irregular and deeply wrinkled, *recessive*).
2. *The colour of the cotyledons,* already dealt with.
3. *The colour of the seed-coat* (grey, grey-brown, or leather-coloured, with or without violet dots, associated with purple-violet flowers and red colouring round leaf-axils, *dominant*; white, associated with white flowers, *recessive*).
4. *The shape of the ripe pod* (not constricted, smooth, *dominant*; constricted between the seeds, *recessive*).
5. *The colour of the unripe pod* (green, associated with green stem, mid-ribs of leaves, and calyx, *dominant*; yellow, associated with similar colouring of stem, mid-ribs and calyx, *recessive*). .
6. *The distribution of the flowers* (scattered along the axis, *dominant*; gathered into a short umber-like cluster, at the extremity of the axis, *recessive*).
7. *The length of the main stem* (tall, *dominant*; short, *recessive*).

The only qualifications Mendel offers, in applying his general statements to these very varied characters, are (1) that the violet dots on the seed-coat are often more numerous and larger in hybrids than in pure-bred forms, and (2) the observation that the mere fact of hybridisation produces an increase in the size of the vegetative organs, so that hybrid plants are often taller than either of their parents, an observation made previously by Knight (No. 18) for peas, and by many later naturalists for peas and other plants (see the summary of the evidence by Darwin, No. 9, Vol. II. Chap. 17, and in addition to the authorities there cited, Naudin, No. 22. For extensive observations on Peas, see Tschermak, Nos. 27 and 28).

It is clearly important to test these remarkable statements by a careful study of the numerical results, and by the application of such tests as may be possible. It seems to me that by neglecting these precautions some writers have been led to overlook the wonderfully consistent way in which Mendel's results agree with his theory, saying that his numbers "are not large enough to give really smooth results," and while they thus unwillingly do rather less than justice to Mendel's own work, at the same time they accept results which seem really inconsistent with those obtained by Mendel as proof that his statements are applicable to a wider range of cases than those he actually observed.

Mendel's observations fall into two groups; the first group relates to a series of cross-fertilisations, in which each pair of races crossed differed in only one of the seven sets of characters dealt with; the second group contains observations on races which differed in two or more sets of characters.

The observations of the first group are more numerous than those of the second, and may be considered first.

The seven sets of observations, showing the dominance of one character in the first hybrid generation, must of course rest upon Mendel's statement, which I think no one who reads his paper will find the slightest difficulty in accepting. The behaviour of hybrids of the second generation can be tested from the numbers which are given. From what has been said concerning yellow and green cotyledons, it is evident that the chance of getting a dominant character in a plant of the second hybrid generation is the chance that one or other of three combinations, out of four which are all possible and equally probable, occurred during the fusion of the gametes which gave rise to the plant. The chance that a given plant of the second hybrid generation will present dominant characters is therefore ¾; and the records may be treated as attempts to verify this experimentally. Now if a series of n things be observed, and the chance that any one of them has a particular character is ¾, the "probable error" of the expectation that ¾n of the things observed will show this character is well known to be 0.67449 $\sqrt{(n \times \frac{3}{4} \times \frac{1}{4})}$; so that if a number of such series are observed, in half of them the frequency with which the desired character occurs will lie between the limits $\frac{3}{4}n \pm 0.67449 \sqrt{(n \times \frac{3}{4} \times \frac{1}{4})}$, and in half of them it will lie outside these limits. In each of Mendel's records of a second hybrid generation the probable error has been calculated, and the result is shown in the following table:

TABLE I.

Individuals with Dominant Characters in the Second Hybrid Generation.

Characters Crossed	Individuals of Second Hybrid Generation	Number of Dominant Individuals	Dominant Individuals on Mendel's Theory	Probable Error of Theory	Deviation of Observation from Theory
1. (Shape of Seeds)	7324	5474	5493	± 24.995	– 19
2. (Colour of Cotyledons)	8023	6022	6017.25	± 26.160	+ 4.75
3. (Colour of Seed Coats)	929	705	696.75	± 8.902	+ 8.25
4. (Shape of Pod)	1181	882	885.75	± 10.037	– 3.75
5. (Colour of Pod)	580	428	435	± 7.034	– 7
6. (Distribution of Flowers)	858	651	643.5	± 8.555	+ 7.5
7. (Height of Plant)	1064	787	798	± 9.527	– 11

Here are seven determinations of a frequency which is said to obey the law of Chance. Only one determination has a deviation from the hypothetical frequency greater than the probable error of the determination, and one has a deviation sensibly equal to the probable error; so that a discrepancy between the hypothesis and the observations which is equal to or greater than the probable error occurs twice out of seven times, and deviations much greater than the probable error do not occur at all. These results then accord so remarkably with Mendel's summary of them that if they were repeated a second time, under similar conditions and on a similar scale, the chance that the agreement between observation and hypothesis would be worse than that actually obtained is about 16 to 1.

The accuracy with which the theory fits the results obtained in the third hybrid generation may be tested in the same way. The plants of the second generation, which exhibit recessive characters, ought to produce offspring which also exhibit only recessive characters, and Mendel assures us that this was the case; of those which exhibit dominant characters, one-third should produce apparently pure-bred offspring of dominant character, two-thirds should produce "hybrid" offspring. The behaviour of plants of the third generation, the offspring of plants with dominant characters, is shown in Table II.

TABLE II.

Proportion of Plants with Dominant Characters, among Hybrids of the Second Generation, which transmitted only Dominant Characters to their offspring.

Characters Crossed	Number of Second Generation Hybrids observed	Number which transmitted only Dominant Characters	Theoretical Number	Probable Error of Theoretical Expectation	Deviation of observed number
1. (Shape of Seeds)	565	193	188.3	± 7.558	+ 4.7
2. (Colour of Cotyledons)	519	166	173	± 7.244	– 7.0
3. (Colour of Seed-Coat)	100	36	33.3	± 3.180	+ 2.7
4. (Shape of Pods)	100	29	33.3	± 3.180	– 4.3
5. (Colour of Pods)	100	40	33.3	± 3.180	+ 6.7
6. (Distribution of Flowers)	100	33	33.3	± 3.180	– 0.3
7. (Height of Plant)	100	28	33.3	± 3.180	– 5.3

Three of these seven determinations give results which differ from that indicated by Mendel's hypothesis by less than their probable errors; the difference between the actual result and that postulated by the hypothesis is equal to the probable error in one case, and greater in three cases; but a discrepancy as great as twice the probable error only occurs once. Here again, therefore, Mendel's statement is admirably in accord with his experiment.

Mendel made several series of observations to test the validity of his statement in cases involving more than one pair of differential characters. The number of possible combinations quickly becomes too great to deal with experimentally, and the most complicated case recorded is that of hybrids between female parents of a race producing round smooth seeds with yellow cotyledons and grey-brown seed-coats, and male parents of a race with angular green seeds and white seed-coats. The original hybrids were 24 in number, and from these 639 hybrids of the second generation were grown and observed. Denoting the dominant characters, roundness, yellowness, and greyness of seed-coat, by A, B, C, and the corresponding recessive characters, angularity, greenness, and whiteness of seed–coat, by a, b, and c respectively, it is clear that the possible combinations of these characters in the hybrids of the second generation are the possible combinations of the three sets of characters

$$AA + aA + Aa + aa,$$

$$BB + bB + Bb + bb,$$

$$CC + Cc + cC + cc.$$

Since there are four combinations of each pair of characters, the number of possible combinations of the three pairs of characters is clearly $4^3 = 64$; and if we consider the union of male dominant with female recessive gametes to be the same as that of female dominant and male recessive, the number of different combinations is 27. Of these 27 different combinations, eight will each occur once, 12 will each occur twice, six will each occur four times, and one will occur eight times, in 64. The combinations actually deduced from the behaviour of the hybrids of the second generation and their offspring occurred with the following frequencies in the 639 plants:

TABLE III.

Frequency of the various possible combinations of Characters in Hybrids of the Second Generation from Races which differed in three Characters.

Combination	Frequency	Combination	Frequency	Combination	Frequency
AABBCC	8	*AABBCc*	22		
AABBcc	14	*AAbbCc*	17	*AABbCc*	45
AAbbCC	9	*aaBBCc*	25	*aaBbCc*	36
AAbbcc	11	*aabbCc*	20	*AaBBCc*	38
aaBBCC	8	*AABbCC*	15	*AabbCc*	40
aaBBcc	10	*AABbcc*	18	*AaBbCC*	49
aabbCC	10	*aaBbCC*	19	*AaBbcc*	48
aabbcc	7	*aaBbcc*	24		
		AaBBCC	14	*AaBbCc*	78
		AaBBcc	18		
		AabbCC	20		
		Aabbcc	16		

These numbers are all correlated, so that the system of results must be judged as a whole. Applying the method of Pearson (No. 25) the chance that a system will exhibit deviations as great as or greater than these from the result indicated by Mendel's hypothesis is about 0.95 (see Elderton, this Journal, *ante*, p. 161), or if the experiment were repeated a hundred times, we should expect to get a worse result about 95 times, or the odds against a result as good as this or better are 20 to 1.

Mendel's statements are based upon work extending over eight years. The remarkable results obtained are well worth even the great amount of labour they must have cost, and the question at once arises, how far the laws deduced from them are of general application. It is almost a matter of common knowledge that they do not hold for all characters, even in Peas, and Mendel does not suggest that they do. At the same time I see no escape from the conclusion that they do not hold universally for the characters of Peas which Mendel so carefully describes. In trying to summarise the evidence on which my opinion rests, I have no wish to belittle the importance of Mendel's achievement. I wish simply to call attention to a series of facts which seem to me to suggest fruitful lines of enquiry.

II. –– OTHER EVIDENCE CONCERNING DOMINANCE IN PEAS.

It is certain that an alternative inheritance, which may produce something like Mendel's phenomenon of segregation, occurs as a result of crossing races of animals and plants, when nothing comparable with dominance can be observed in the immediate offspring of the cross. The two phenomena must therefore be considered separately (cf., Correns, No. 5).

The evidence concerning dominance in the first hybrid generation of Peas relates chiefly to the colour of cotyledons and seed-coat, and to the shape of the hybrid seed. In judging it, we must be careful to realise what the statement, that a character is dominant, really means. Many races of Peas are exceedingly variable, both in colour and in shape. A race with "round smooth" seeds, for example, does not produce seeds which are exactly alike; on the contrary, many seeds of such a race as *Victoria*, used by Rimpau (No. 26) as a typically round and smooth-seeded Pea, or *Express* used by Tschermak (No. 27) in the same way, show very considerable irregularities; while in races such as *Prince of Wales* or *Telephone*, used by Tschermak and others as types of races with wrinkled seeds, hardly any two seeds are alike. So that both the category "round and smooth" and the category "wrinkled and irregular" include a considerable range of varieties. At the same time, the categories are undoubtedly often discontinuous, the most wrinkled seed of such a race as *Express* or *Victoria* being so much smoother and more rounded than the most regular seed of the typically "wrinkled" races, that no one who knows both races would hesitate for a moment in deciding which race a given seed resembled.

The statement that smoothness of seed is dominant over the production of wrinkles means therefore that if a parent, belonging to a variable race which falls into the category "smooth-seeded," be crossed with a parent belonging to a variable race of the category "with wrinkled seeds," the offspring will themselves be variable, but will always belong to the category "smooth-seeded": and as it is with shape, so it is with colour.

The first detailed account of the *colour* in hybrid Peas, which I have been able to find, is that of Goss, 1848 (No. 15), who fertilised the flower of a "blue-seeded" race with pollen of a race with yellowish white seeds. The hybrid seeds were all yellowish white; and the plants raised from them "produced some pods with all blue, some with all white, and many with blue and white seeds in the same pod"; or the result was probably that obtained by Mendel. In a note to this paper, the then Secretary of the Horticultural Society says that 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. In 1849 Gärtner (No. 12, pp. 81–85) described the result of crossing races of Peas; the yellow-seeded *Pariser Wachserbse* which he calls *Pisum sativum luteum*, was fertilised (*a*) with pollen of *P. sativum macrospermum* which had seeds of an impure greenish-yellow, and (*b*) with pollen of the green-seeded *P. sativum viride*. In the first case the hybrid seeds were all pure yellow; in the second case twelve seeds were produced in four hybrid pods; and these were all of a greenish-yellow colour, although the greenish tinge disappeared from some of them on drying. Another yellow-seeded Pea (*P. sativum nanum repens*) fertilised with the pollen of the green-seeded *P. sativum viride* gave five hybrid pods with seeds, of which one contained five dirty green seeds, a second had five seeds which were "not distinctly yellow, but yellowish green," although they lost their greenness after being dried for two months. The others were not yellow like the mother, but "dirty yellow." It is clear that the "greenness" of *P. sativum viride* did in these cases affect the colour of the seeds, when its pollen was used to fertilise plants of yellow-seeded race, though it is difficult to judge exactly how great the effect was. The disappearance of the green colour on drying may have been simply due to the development of an air-space between the seed-coat and the cotyledons, which as Tschermak (No. 27) has pointed out may obscure the colour of the cotyledons in the dry seed, or it may have been due to a real increase in yellowness. The flowers of *P. sativum viride* were fertilised with pollen from two pure yellow-seeded races (*P. sativum luteum* and *P. sativum nanum repens*), and in the first case the seeds produced were "not distinctly yellow, still less blue or green, but dirty yellow." In the second case the seeds produced were yellow; and when *P. sativum viride* was fertilised by *P. sativum macrospermum* the seeds produced were apparently yellower than those of the male parent.

The effect of the dominance of yellowness over greenness of cotyledons in hybrids of the first generation, if it were indeed universal, would be so striking that one can hardly conceive that the great founders of our modern races of Peas, such as Knight (No. 18) and Laxton (No. 19), should have failed to notice it, and yet neither of them, in describing experience gained from crossing great numbers of plants, says that it is of general occurrence.

The colour of seeds of the first hybrid generation has not, so far as I can discover, been carefully described between the time of Mendel and the year 1893, when Giltay (No. 14), who does not appear to have known Mendel's work, crossed several yellow-seeded peas with the green-seeded race *Reading Giant*, and found that the colour of the cotyledons was always yellow, showing that Mendel's law of dominance was completely valid in this case. (Giltay points out the necessity of removing the seed-coats before determining the colour of the cotyledons; this is also emphasised by Tschermak, and I have found it quite necessary even in seeds of pure race.) In 1900 general attention was directed to Mendel's work, and the result of crossing Peas has lately been described by Correns (Nos. 3 and 4) and in greater detail by Tschermak (Nos. 27 and 28). Correns confirms Mendel's statements concerning the dominance of yellow cotyledons, but Tschermak makes a more detailed statement, which does not so fully agree with Mendel. It is not quite easy to follow Tschermak's account, because he does not describe all his very numerous and careful experiments in such a way that one can be sure how many hybrid peas he observed. He certainly crossed between 80 and 100 flowers, belonging to green or yellow–seeded races, with pollen from plants with seed of the opposite colour, obtaining between 300 and 400 hybrid seeds. Of these hybrid seeds about 40 were not distinctly yellow, so that 90 per cent. of the hybrids exhibited the dominant character. Of the seeds which did not exhibit this character, some were yellow with green patches, eight were green, four were "yellowish green," and five are described as showing "Grün und Uebergänge von Gelb zu Grün," so that while some 10 per cent. of the hybrids did not exhibit dominance of yellow, some 2 or 3 per cent. exhibited a close approximation to the character of the "recessive" parent. A further case is recorded by Tschermak, where a plant of the yellow-seeded variety *Buchsbaum*, growing in the open, produced a pod in which every pea except one was green, the exception showing a little yellow. One of the green seeds was sown, and the plant produced fifteen yellow and three green seeds, thus behaving like a hybrid. Tschermak considers that this is a case of accidental crossing, with dominance of green, and although some of the green peas, produced in his experiments, may have been due to accidental self-fertilisation, he regards some of them, at least, as hybrids (cf. No. 28, pp. 663-664). It should be said that some of the crosses referred to were made between the (yellow-seeded) *P. arvense*, var. *Graue Riesen*, and green-seeded varieties of *P. sativum*. In all such crosses the law of dominance of yellow held absolutely.

These results show clearly enough that the law of dominance is, as Tschermak says, not absolutely true of cotyledon colour, and as will presently be shown, the exceptions to the law, which he observed, form a very large percentage of the total result obtained when certain races were crossed.

The case of cotyledon colour has been considered first, because the evidence with regard to it is more favourable to Mendel than is the evidence touching other seed characters. The *shape* of seeds, whether smooth and rounded or irregular and wrinkled, is even more difficult to express in words than the colour of their cotyledons, and the varieties appear to be even less constant. The evidence against the universal validity of the law of dominance is here much stronger than in the case of cotyledon-colour. Two striking cases were observed by Rimpau (No. 26, pp. 36, 37), who crossed the smooth-seeded race *Victoria* with two wrinkled races, *Knight's Marrow* and *Telephone*. He made each cross in both the possible ways, and found the second hybrid generation dimorphic, as usual. From the cross *Victoria* ♀ × *Knight's Marrow* ♂ he obtained round and wrinkled seeds of the second generation, as Mendel's statements would lead us to expect. The wrinkled seeds were sown, and produced both round and wrinkled seeds, the wrinkled (recessive) character becoming "true" only in the fifth year. The wrinkled seeds of the second generation from the cross *Victoria* ♀ × *Telephone* ♂ also gave rise to plants with rounded and wrinkled seeds; but the descendants of these were not observed. If Mendel's law of segregation was here followed, his law of dominance was not; because if both are valid, a plant of the second hybrid generation which exhibits recessive characters must behave, so far as those characters are concerned, like a pure-bred individual. The most careful account of seeds of the first hybrid generation is that of Tschermak, in the papers already quoted. The variety *Telephone* especially, when crossed with smooth-seeded varieties, gave a large number of wrinkled seeds, or seeds of intermediate character. Thus the *Pois d'Auvergne* used by Tschermak had the ripe seeds "always round and smooth"; but out of 27 seeds recorded from seven crosses between this pea as the ♀ and *Telephone* as ♂ parent, nine were slightly wrinkled, and two out of ten resulting from the reciprocal cross were slightly wrinkled. These are difficult cases to judge; but the cross *Telephone* ♀ × the smooth-seeded *Plein le Panier* ♂ gave seeds which "differed only slightly from those of the mother," although the wrinkles were perhaps not so deep. Again, *Telephone* ♀ × the smooth *grün-bleibende Folger* ♂ gave seeds which certainly belonged to the category "wrinkled," although they were more rounded than those of pure *Telephone*. After pointing out the exceptions to dominance of yellow cotyledon-colour already mentioned, Tschermak summarises his view of the dominance of wrinkles as follows:

> Auch in Bezug auf die Form fehlt es nicht an Fällen, in denen sich das sonst dominirende mit dem sonst recessiven Merkmale in einem gewissen Verhältnisse combinirte. So ergiebt *im Allgemeinen* die Bestäubung einer gerunzelten Markerbse mit Pollen einer glattsämigen Varietät abgerundete, schwach gerunzelte Produkte, und zwar eher als die umgekehrte Verbindung der Eltern.

This is a sufficient statement of Tschermak's result, so far as it concerns races of *P. sativum*. Correns (No. 3) found that the *grüne späte Erfurter Folger-Erbse* which has round smooth seeds, was not dominant in this respect over the *Pahl-Erbse mit purpurrothen Hülsen*.

The foregoing crosses show that the law of dominance does not always hold for the shape of seeds, when the races crossed belong to the species *P. sativum*. The race of *P. arvense* called *Graue Riesen* is held by some botanists to belong to a different "species," and may therefore be considered separately. 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 *P. arvense* in shape, although in colour they follow Mendel's law of segregation!

The discussion of *seed-coat colour* is more difficult than that of the two characters already dealt with, because the recent writers (especially Tschermak) pay attention to a character, namely green pigment in the seed-coat, which Mendel does not mention. It is clearly unreasonable to expect that every character in the seed-coat should obey the same law, and therefore in trying to estimate the agreement between Mendel and later workers, many valuable data collected by Tschermak will be neglected. The most striking exception to the law of dominance is that observed by Correns. The *grüne späte Erfurter Folger-Erbse* has a nearly colourless seed-coat (recessive, Mendel); the *Purpurviolettschottige Kneifel-Erbse* and the *Pahl-Erbse mit purpurrothen Hülsen* have the seed-coat uniformly orange, becoming brown with age. In hybrids of the first generation, between either of these last varieties and the *Erfurter Folger-Erbse*, the coats of seeds (often in the same pod) were sometimes nearly colourless, sometimes intensely orange-red, but generally more or less orange-red, and spotted more or less strongly with blackish violet. The seeds of extreme colour, those with orange or those with almost colourless seed-coats, gave plants of the second generation which again showed the same extremes of colour in the seed-coats, connected by transitional forms. This is clearly a case in which one of Mendel's characters obeys neither the law of dominance nor the law of segregation.

The appearance of blackish-violet dots on the seed-coats of similar hybrids was noticed by Mendel. In his crosses however one parent showed traces of such dots, which were only exaggerated in the offspring. In the plants used by Correns as parents, the seeds with brown coats are not said to have possessed these dots. An exaggeration of the purple dots, of a kind similar to that observed by Mendel, but even greater in degree, was found by Tschermak in crosses between *Graue Riesen* and varieties of *P. sativum* with colourless seed-coats.

Enough has been said to show the grave discrepancy between the evidence afforded by Mendel's own experiments, and that obtained by other observers, equally competent and trustworthy. It does not seem to me reasonable to doubt the substantial accuracy of any of the statements made by the observers quoted. I have deliberately refrained from collecting the numerous scattered records of odd crosses which exist in the various journals devoted to horticulture, because many of these are published either anonymously or by persons whose skill in performing the difficult operation of crossing in such a way as to be sure of the result may possibly be doubted. The evidence brought together rests upon the statements of men whose knowledge and skill are beyond question, and the only conclusion which can, I think, be fairly drawn from it is, that dominance of any of the characters mentioned is not an invariable attribute of the character, but that a cross between pairs of parents, such that the different members of each pair differ to the same extent in cotyledon colour or in similar characters, may in different cases lead to widely different results, and one great reason why this is so becomes evident on a little consideration.

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 all 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 difference 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 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.

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. 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 quite clear from Tschermak's paper whether *all* the seeds were of this colour, but certainly some of them were.] The green *Plein le Panier* ♀ × *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 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 ancestor. 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 in every case with a very definite combination of ancestral characters, and had no proper basis for generalisation about yellow and green peas of any ancestry.

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 patchwork 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.

This neglect of ancestry, the tendency to regard offspring as resembling their parents rather than their race, accounts for much of the apparent inconsistency between the results obtained by different observers who have crossed plants or animals.

The writer who has most clearly recognised the importance of ancestry in connection with Mendel's work is Correns. In a recent summary of his views (No. 6) and in his fuller account of experiments in crossing races of Maize (No. 7) be says that between the complete equivalence of two characters and the complete dominance of one of them, all intermediate stages may exist, and that the dominance of a character varies (*a*) according to the individuality of different gametes from the same gonad; (*b*) according to the individuality of the different plants of the same race; (*c*) according to the race of the plant. He also points out that the offspring of pure-bred races differ in their power of transmitting "alternative" characters (which Correns, adopting Mendel's theory of the constitution of gametes in this case, calls schizogonic) from the offspring of a cross, although the apparent characters of both may be the same. Correns illustrates and justifies his statements by detailed accounts of experiments with Maize; and his figures of parti-coloured heads of seed, produced by fertilising a white-seeded female flower with pollen from a single male flower of blue-seeded race are most striking. They show that the result may be either a blue seed, or a white seed, or a piebald white and blue seed, or a seed of uniform but intermediate colour. The peculiar process of double fertilisation to which this change of colour in the extra-embryonic tissues of Maize is due does not seem to me to affect the relevance of the observations.

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.

Correns (No. 5) himself has crossed the Stock *Matthiola annua* = *M. incana* D.C., which has its green parts covered with grey hairs, and the smooth-leaved Stock, *M. glabra* D.C. The 111 hybrids obtained from reciprocal crosses all had hairy leaves. Trevor Clarke made a similar cross, using of course different races, and found that half his seedlings had smooth leaves, half had hairy leaves (No. 2).* Again, the petals of the *M. incana* used by Correns were violet, those of the *M. glabra* were yellowish white. The petals of the hybrid seedlings were invariably either violet of the shade of *M. incana*, or violet more or less obviously spotted with pale violet. On the other hand, Nobbe (No. 23) crossed a number of varieties of *M. annua* in which the flowers were white, violet, carmine–coloured, crimson, or dark blue. These were

* According to Bateson (*Journ. Roy. Hort. Soc*. Vol. XXIV. p. 64), Miss Saunders has obtained a similar result. Correns doubts whether Trevor Clarke's flowers were completely cross-fertilised.

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 case, but it is clear that the colours blended.

Again, de Vries (Nos. 30 and 31) whose evidence for most of his statements concerning the validity of the law of dominance has not yet been published, crossed *Datura tatula* with the smooth-fruited form of *D. stramonium*. *D. tatula* has blue or violet flowers, and dull purple stems; the flowers of *D. stramonium* are white and its stems bright green. De Vries found that in all his hybrid seedlings the flowers were blue, and he concludes that the colouring of *D. tatula* is dominant in Mendel's sense. Naudin (No. 22) crossed *D. tatula* with the variety of *D. stramonium* which has spiny fruit and white flowers. The flowers of his hybrids were violet, but paler than those of *D. tatula*, and their stems were flushed with purple, but to a less extent than those of *D. tatula*; so that in his crosses a blending of the parental colours occurred. Again, de Vries found that the fruit of his hybrids was spiny, and concludes that the production of spines is a dominant character. Naudin crossed the smooth-fruited and the spiny-fruited forms of *D. stramonium* (which he called distinct "species") and found that among the fruits of forty hybrids some were completely spiny; others were smaller than the normal fruits of the spiny form (in this resembling the smooth form), while their spines were shorter and weaker than in the pure spiny form; others again were a mosaic of smooth and spiny segments. On the other hand, *D. stramonium* of the spiny form, crossed with *D. ceratocaula*, which has a smooth fruit of different character, gave hybrids whose fruits exactly resembled those of *D. stramonium*.

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. Many people have crossed the various white, piebald and wild-coloured varieties of the rat (*Mus decumanus*), the closely similar varieties of the mouse (*Mus musculus*) have also been frequently crossed. In both rats and mice von Fischer (Nos. 10 and 11) 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. Crampe (No. 8) finds that in either case the offspring are a mixture of piebald forms and albinos. Results such as those which Crampe records in rats are commonly obtained when piebald and albino mice are paired; but both

Haacke (No. 17) and von Guaita (No. 16) find that when the ordinary European albino mouse is paired with the piebald Japanese “dancing” mouse, the offspring are either like wild mice in colour, or almost completely black. Again, Crampe says that when white and wild-coloured mice are crossed the offspring are invariably coloured like wild mice. Colladon is reported by Prévost and Dumas (*Ann. Sci. Nat.* I, 1824) to have obtained both albino and wild-coloured individuals from similar crosses, but no piebald individuals.

These examples, chosen from many others which might have been cited, seem to me to show that it is not possible to regard dominance as a property of any character, from a simple knowledge of its presence in one of two individual parents. 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. A collection of cases which illustrate this point is given by Bateson (No. 1).

III. — THE HYBRID PEAS OF THE TELEPHONE GROUP.

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. In attempting to follow the results obtained by Tschermak and others I have carefully examined the seed characters of some twenty named varieties, and the present condition of many I have studied seems to me quite incompatible with the general validity of Mendel’s statements. The aberrant behaviour of the race called *Telephone* has already been observed by Rimpau and Tschermak, and I have therefore endeavoured to learn the past history and the present condition of this Pea and the races allied to it. In my attempt I have received very great help from Messrs Carter and Co., who originated *Telephone* and its allies, from Messrs Sutton and Sons, and from Messrs Vilmorin-Andrieux and Co., of Paris. All these gentlemen have supplied me with quantities of seeds of various races, and have spent much time and trouble in answering questions concerning them. I gladly take this opportunity of expressing my gratitude to all of them, and especially to Messrs Carter and Co., the value of whose help will be presently apparent.

In 1876 Culverwell introduced into the English market a Pea which he called *Telegraph*. This was a hybrid race, and he says that his stock was derived from a single cross-fertilised flower. The stock of *Telegraph* was ultimately bought by Carter and Co., who found it so variable that without further crossing they produced from it, by simple selection, the four races now known as *Telephone*, *Stratagem*, *Pride of the Market*, and *Duke of Albany*. These four races, together with *Telegraph*, are still cultivated, and I have examined them all. Their history is well known, and is authenticated not only by Carter's records, but by letters of Culverwell, and by Laxton (No. 20). Between 1880 and 1890 Carter and Co. crossed *Stratagem* with *Giant Marrow*, another of Culverwell's races; and the offspring of this cross was introduced into the market in 1892 as *Daisy*. A few years later the race *Daisy* was crossed with *Lightning*, a Pea which has round, nearly smooth seeds, and yellow cotyledons. The result of this cross is known as *Early Morn*. Culverwell's *Giant Marrow* is not now easy to obtain; but all the other races referred to are grown commercially, on a large scale, and I have examined the characters of their seeds.

In attempting to judge the results of other observers. including those of Mendel himself, I have constantly found it difficult to understand the statements made, because of the vagueness of the terms used to describe shape and colour. In order to make my own statements about colour as intelligible as may be, I selected from a sample of *Telephone* grown by Carter a series of 18 peas, which show, after removal of the seed-coats, a fairly gradual series of transitional colours from a deep green to an orange yellow. These seeds were arranged in groups of three, so that six colour-groups were formed; and these groups, numbered from one to six, the first being green and the sixth orange-yellow, form a scale in terms of which I shall express the colour of all the peas described. The groups are represented in Figs. 1-6 on Plate I. [Peas of all these colours are numerous, as are peas exhibiting the other characters shown on the plate: and I shall have much pleasure in sending a replica of the set from which the plate was photographed to any naturalist who may write to me before my stock is exhausted.]

In the same way, I have tried to make my statements about the shape of seeds intelligible by means of the photographs reproduced on Plate II.*

(1) *Telegraph* was at first very variable, both in shape and in colour, and *Telephone* did not become thoroughly differentiated from it for some years. In 1878 the Royal Horticultural Society gave a certificate to *Telephone* as a new variety, and in 1879 a controversy arose as to the reality of the distinction between the two. The Editor of the *Gardener's Chronicle* (1879, p. 210) says, "It is clear that what Messrs Carter and Co. are sending out as *Telephone* is the most wrinkled seed selected from *Telegraph*," and later in the same year

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* Plates I. and II. will be found on p. 29.

(August 2nd, p. 146) the Editor describes seeds sown at his direction in order to test the identity of the two races. Among the seeds sown are three samples of *Telegraph*. In one the seeds are said to be "mixed, round and wrinkled," in the second and third they are "but slightly wrinkled." And since on the one hand the seeds of *Telephone* are admittedly "wrinkled," while on the other hand there is some doubt whether *Telegraph* and *Telephone* are really distinct, it is clear that the offspring of the hybrid *Telegraph* had not become sharply divided into a smooth-seeded and a wrinkled race in 1879, as they should have done on Mendel's hypothesis. The presence of forms intermediate between the categories "round" and "wrinkled" in 1879 seems proved by the fact that the controversy referred to arose. The *Telegraph* of to-day is more than 25 generations removed from the original cross, and it should, on Mendel's view, have split into two groups, one with seeds completely smooth and rounded, the other with wrinkled seeds. Seeds of intermediate type should not occur, and only one plant out of every $2^{25} - 1$, or say one plant in every thirty-three millions, should bear seeds of both kinds.

As a matter of fact, the seeds of *Telegraph* as grown by Carter and Co. exhibit every conceivable condition between the perfectly smooth forms shown in Fig. 1, Plate II., and the forms with well-marked wrinkles shown in Fig. 4 on the same plate. The groups photographed in Figs. 1-4 were chosen from a single quart of *Telegraph* given to me by Messrs Carter; and a rough estimate of the relative frequency with which the characters of each group occurred in a small sample gave the following result:

Group 1 ………………………	242
Group 2 ………………………	228
Group 3 ………………………	28
Group 4 ………………………	2
	500

It is not suggested that the groups differ successively by approximately equal increments of wrinkles, so that the scale they form is certainly imperfect. The grouping of the peas is also very rough. But with all these defects the study of *Telegraph* seems to me to demonstrate that the offspring of a hybrid Pea, 25 generations at least after crossing, may contain a large percentage of individuals which on Mendel's view that roundness is dominant ought never to occur at all.

The distinction in colour between *Telegraph* and *Telephone* was also discussed twenty years ago. The seed-coats are often so opaque in all these races, that it is difficult to estimate cotyledon colour from descriptions of the pea with its seed-coat uninjured. A statement by Culverwell seems however worth quoting. In 1882 he writes of *Telegraph* and *Telephone*: "The two will always come from one sort, more especially from the green variety." And a line or two later, describing the result of sowing what he thought a good sample of *Telegraph*, he says, "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." (*Gardener's Chronicle*, July 1882, p. 150.)

This is only one of a number of statements, scattered through the *Gardener's Chronicle* from 1879 onwards, which show that neither *Telegraph* nor *Telephone* was recognised as sharply divided into green or blue and yellow or white races during the early years of their existence; Culverwell's statement that the green variety was especially variable in colour in 1882, shows more than this, however, because it shows that in his opinion a plant of a late generation, which exhibited a "recessive" colour, did not produce exclusively recessive offspring, as Mendel says it should. At the present day they are recognisably distinct, both in shape and in cotyledon colour; but the colour of the cotyledons is variable in both. Using the groups of seeds photographed on Plate I. as a scale, I found among 576 seeds of *Telegraph*, 512 seeds of fairly uniform colour, and 64 obviously piebald seeds. The self-coloured seeds fell into one or other of the colour groups from 1 to 6, with frequencies given in Table IV. (p. 26). The piebald remainder were generally half bright yellow and half bright green. There were generally only two patches of colour on each seed, and one cotyledon was often as yellow as Group 6, Plate I., while the other was as green as Group 1.

(2) *Pride of the Market*. If shape and colour be considered together, this is one of the most constant races selected from the off-spring of *Telegraph*. Of 500 seeds whose shape was examined, there were

Like	Fig. 1	……………..	260		
”	Fig. 2	……………..	218		
”	Fig. 3	……………..	20	or	21
”	Fig. 4	……………..	2	or	1

while the colour, as shown in Table IV., is distinctly less variable than in *Telegraph*, and the percentage of piebalds perhaps significantly smaller.

(3) *Stratagem* is nearly as constant as *Pride of the Market* in colour, but it is more variable in shape. The seeds are larger than those of any other race belonging to this group, and are normally much

flattened; for this reason it is difficult to compare the seeds of *Stratagem* with those of the races just described. Three groups of *Stratagem* seeds are photographed in Figs. 7, 8 and 9 (Plate II.) and they show the characteristic shapes and wrinkles fairly well. An inspection of Figs. 1-9 will show better than any words, *first* how completely the categories "smooth" and "wrinkled" pass into each other in these races; and *secondly* how enormously the range of variation included under the two differs.

The colour of *Stratagem* is interesting because of its intermediate condition between the extremes observed in the group of races to which it belongs. As will be seen from Table IV., piebald seeds are rarer than in any of its allies, and the great majority of seeds fall into the colour-groups 2 and 3*, with a very small percentage of seeds so green as Group 1, or as yellow as Groups 4 and 5. The general impression produced by a mass of these seeds, when stripped of their coats, is certainly green; but it is a far yellower green than that of either *Telegraph* or *Pride of the Market*; and I think there can be no question that in *Stratagem* a blend of green and yellow has been inherited, and fixed by a process of selection.

(4) *Telephone*, in the samples given to me by Carter and Co. or by Sutton and Sons, is fairly uniform in shape, being practically always as wrinkled as Figs. 5 and 6. It appears however from Tschermak's account (No. 27, p. 480) that samples which he bought in Ghent and in Quedlinburg were more variable, and contained smoother, more oblong forms. The same thing is true of a sample which I bought in Oxford from Messrs McGreal and Co. The colour of all the samples I have seen (from Vilmorin-Andrieux, Carter, Sutton, and McGreal) is exceedingly variable. Every one of the six colour-groups is abundantly represented, and indeed the scale of colours, which was found suitable for the whole series of races, was selected from this race alone. There can be no question that self-coloured seeds of every shade intermediate between the darkest green of Fig. 1 and the most intense orange-yellow of Fig. 6 occur in every large sample of this race, while piebald peas, with every degree of difference between the colours of their patches, occur also. Groups of piebalds, illustrating their main characters, are shown in Figs. 13-18 on Plate I. The colour variation of this race, together with Tschermak's description of its behaviour when crossed as a green-seeded pea with exceptional dominance, led me to tabulate the colours in several samples. The results are given in Table IV.; and while the different samples differ considerably among themselves, they

* As will be seen from Plate I, Figs. 7-12, many seeds of this race are intermediate in colour between Figs. 2 and 3.

all show the same general characters. In all of them the range of colour is the whole range of the scale, and the groups of intermediate colour occur most frequently; in all of them there is a large percentage of piebald individuals. It is evident that in a very large percentage of these individuals the characters "green" and "yellow" are perfectly blended, while others present a mosaic or piebald character; but even in these piebald individuals the patches of colour cannot, in some cases, be spoken of as pure green or pure yellow; the pea may exhibit a blend of green and yellow on every part of its surface, but the proportions in which the two are mixed may differ in the two cotyledons, or in different parts of the same cotyledon. The suggestion that yellow and green are mutually exclusive alternatives, or that anything like Mendel's phenomena of dominance and segregation has occurred in the history of *Telephone*, is clearly absurd.

(5) *Duke of Albany* resembles *Telephone* so closely in the general characters of its seeds, that I have only examined a small sample, sent to me by Messrs Sutton and Sons. The frequency of colour varieties in this sample is given in Table IV.

(6) *The Hybrid Descendants of Stratagem.* It has already been pointed out that the average colour of *Stratagem* must be regarded as a blend of yellow and green. The yellow properties of this blend are well seen in *Daisy*, the result of the cross *Stratagem* × *Giant Marrow*. In shape, the seeds of *Daisy* are generally oval, with two opposite concave faces, the whole surface being wrinkled to a variable extent. Forms intermediate between this and the thinner flattened form of *Stratagem* also occur, as do more rounded forms. The chief shapes may be gathered from Figs. 9 and 10 (Plate II.). The average colour is a fairly uniform green; but as will be seen from Table IV., piebald individuals, and individuals of colour 4, occur.

Daisy and *Lightning* were crossed, as has been said, to produce the race *Early Morn*. In its present condition *Lightning* is a very round and smooth-seeded Pea, the shapes which occur being shown in Figs. 13 to 15 (Plate II.). The wrinkles of the group photographed in Fig. 15 occurred in about 16 out of 250 seeds examined. The colour varieties include a small percentage of green and piebald seeds; but the great majority of the seeds are of a deeper orange than that of Group 6. *Lightning* is what I imagine most of the writers on Mendel's laws would accept as a typical round, smooth, yellow Pea. The seeds of the second generation (produced by the first hybrid plants) were variable both in shape and colour. Messrs Carter and Co. have circulated reproductions of a photograph of one pod, containing peas of the second generation. The pod contains seven seeds, of which three are labelled "white," three "blue," and one "green." Two of the seeds seem smooth, while the rest are wrinkled in various degrees. By the kindness of Messrs Carter and Co. I have been able to examine a sample of *Early Morn* not as it is now, but as it was when they introduced it. The race was apparently selected from seeds of the second hybrid generation which were "recessive" both in colour and in shape; and although we must remember that the seed saved when making the stock from which a new race might be established was selected, and cannot be supposed to represent all the seed produced by the offspring of all the green and wrinkled hybrids, yet so far as the evidence available goes it favours the view that the offspring of wrinkled seeds were themselves wrinkled, for the sample given to me contains only wrinkled seeds of fairly uniform character. These seeds do not in the least resemble the seeds of *Daisy*. As will be seen from Figs. 16-18 (Plate II.), they are far more like those of *Telephone* in the character of their wrinkles than they are like either of their parents. This is another example of the danger incurred by using Mendel's categories without careful examination. The statement that the seeds of *Daisy* and *Early Morn* are wrinkled and irregular, while those of *Lightning* are fairly smooth and rounded, is perfectly true; but if made in this form, without further explanation, it suggests a likeness between *Daisy* and *Early Morn* which does not exist. So far, as the shape of *Early Morn* exhibits a reversion to any of its known ancestors, the reversion is directly to the most wrinkled type of the original *Telegraph*. In sending me the sample I have examined, Messrs Carter wrote of *Early Morn*: "You will clearly see the trace of the white Pea which was one of its parents." The analysis of the colour variations, given in Table IV., abundantly confirms Messrs Carter's statement: the majority of seeds are green; but seeds of intermediate colour, and piebald seeds, do occur with quite sensible frequency.

TABLE IV.

Frequency of Colour Variation.

Race	Colour 1	Colour 2	Colour 3	Colour 4	Colour 5	Colour 6	Piebald	Total
Telegraph	354	95	47	10	4	2	64	576
Pride of The Market	447	76	19	2	2	1	55	602
Stratagem	200	367	154	16	5	0	40	602
Telephone (Carter)	191	289	195	59	38	38	133	943
" (Sutton)	13	83	112	32	15	13	43	311
" (Vilmorin)	29	69	69	23	3	2	5	200
Duke of Albany	26	70	121	53	11	20	27	328
Daisy	78	175	27	7	0	0	17	304
Early Morn	267	239	81	2	1	1	9	600

IV. — MENDEL'S LAW OF SEGREGATION.

The history of the Telephone group of Peas is clearly inconsistent with the universal validity of Mendel's laws of dominance and segregation. The hybrid *Telegraph* produced seeds of various colours at the time of its origin, and now, more than five-and-twenty years after its introduction, it does so still. From the variable offspring of this hybrid races have been produced by selection, which bear either yellow-green seeds of fairly constant character (*Stratagem*) or a mixture of self-coloured and conspicuously piebald seeds, the self-coloured seeds presenting every conceivable colour between deep green and intense orange-yellow (*Telephone*). These races are many generations removed from their common hybrid ancestor, and it may be suggested that phenomena such as those described by Mendel could have been observed in the earlier generations No decisive answer to such a suggestion can now be obtained; but the hybrids *Daisy* and *Early Morn* are both little removed from their cross-fertilised ancestor; in their present selected form both exhibit characters which should, on Mendel's view, be recessive, and should therefore produce invariably recessive offspring, while in fact their offspring is variable.

The behaviour of these races is much more exactly in accord with the statements of Laxton. In 1866, the year in which Mendel's paper was published in printed form, Laxton published a short summary of the results gained during many years of work upon Peas, which shows that his experience was altogether different from that of Mendel. He says of the colour and character of the seed:

> 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, that is to say, seed produced from the second 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. (Laxton, No. 19, p. 156)

In a review of his own work, nearly a quarter of a century later, Laxton says again: "By means 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." (No. 20.)

These statements show that the phenomena of inheritance in cross –bred Peas, as Laxton observed them, were far more complex than those described by Mendel; but they do not preclude the possibility of a simple segregation, such as Mendel describes, in particular cases. Such cases of simple segregation have been described in Peas by both Correns and Tschermak in the papers already cited. The proportions of dominant and recessive individuals, found by Correns in his later generations, were in accord with Mendel's results; those found by Tschermak, as he himself points out, were extremely improbable, on Mendel's hypothesis.

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. The law of segregation, like the law of dominance, appears therefore to hold only for races of particular ancestry. In special cues, other formulae expressing segregation have been offered, especially by De Vries (32) and by Tschermak (29) 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 apparently 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.

PLATES.

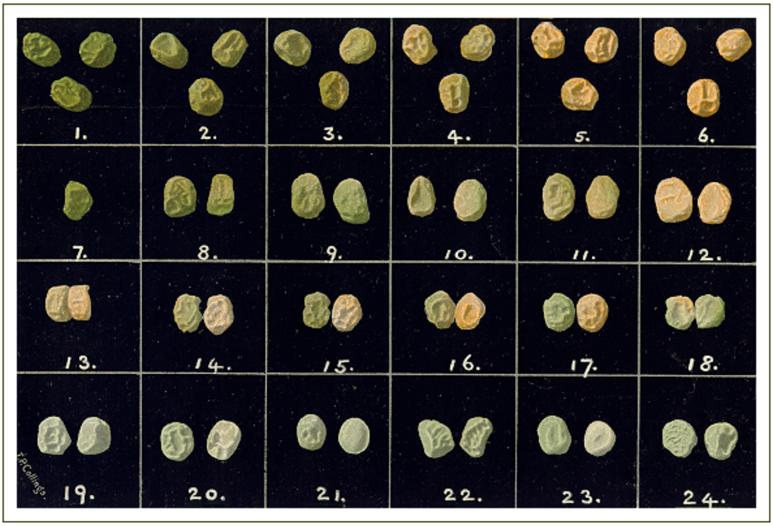

Plate I.

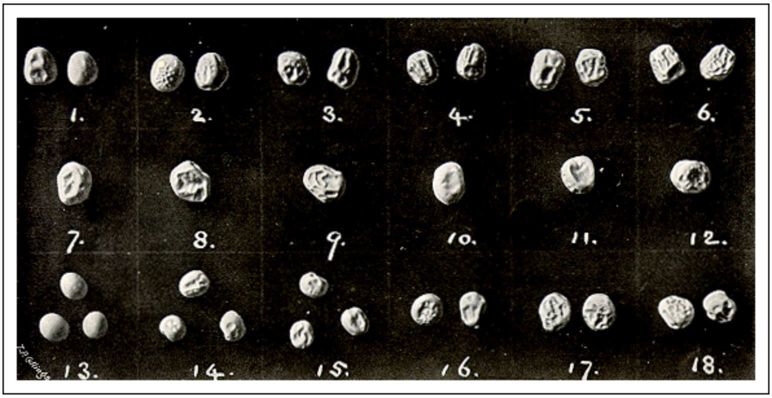

Plate II.

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