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

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

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

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

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

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

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

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

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

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

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

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

* Correns found a similar result.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

C. Evidence of Knight and Laxton.

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

The first is that of Knight's well-known experiments, long familiar but until now hopelessly mysterious. I have not space to quote the various interpretations which Knight and others have put upon them, but as the Mendelian

principle at once gives a complete account of the whole, this is scarcely necessary, though the matter is full of historical interest.

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

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

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

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

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

† As heterozygotes often do.

‡ Dominance of the purple form.

§ Dominance of the grey coat as a maternal character.

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

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

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

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

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

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

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

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

† Tall heterozygotes, with normal dominance of purple flowers.

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

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

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

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

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

† As, commonly, in heterozygotes when fertile.

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

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

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

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

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

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

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

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

‡ Pure recessives.

§ Pure recessives in coats showing maternal dominant character.

‖ Now recognized as pure homozygotes.

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

** Being now homozygotes.

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

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

* Being heterozygotes exclusively.

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

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

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

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

‡ Cotyledons seen through coat.

§ Ordinary dominance of round.

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

¶ If we were obliged to suppose that this is a matured conclusion based on detailed observation it would of course constitute the most serious "exception" yet recorded. But it is clear that the five

would seem to indicate that the white round and the blue wrinkled peas are distinct varieties derived from ancestors respectively possessing one only of those marked qualities; and, in my opinion, the white round peas trace their origin to a dwarfish pea having white flowers and round white seeds, and the blue wrinkled varieties to a tall variety, having also white flowers but blue wrinkled seeds. It is also noticeable, that from a single cross between two different peas many hundreds of varieties, not only like one or both parents and intermediate, but apparently differing from either, may be produced in the

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

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

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

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

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

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

* See later.

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

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

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

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

D. Miscellaneous cases in other plants and animals.

Professor Weldon proceeds:

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

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

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

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

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

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

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

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

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

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

Note then

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

So once again Professor Weldon suggests that his laws of ancestry will explain even the discrepancies between von Fischer on the one hand and Crampe and von Guaita

on the other but he does not tell us how he proposes to apply them.

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

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

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

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

* Excluding "false hybridisations."