ROYAL SOCIETY

REPORTS TO
THE EVOLUTION COMMITTEE

Report I.

Experiments undertaken
by
W. Bateson, F.R.S., and Miss E. R. Saunders

LONDON
HARRISON & SONS, ST. MARTIN'S LANE
Printers in ordinary to his
Majesty.
1902.

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M. A. Willcox

REPORTS TO THE EVOLUTION COMMITTEE OF THE ROYAL SOCIETY.

REPORT I.—EXPERIMENTS UNDERTAKEN BY W. BATESON, F.R.S., AND MISS E. R. SAUNDERS.

(Presented to the Committee, Tuesday, December 17, 1901.)

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EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY.

By W. Bateson, M.A., F.R.S., and Miss E. R. Saunders, Lecturer, Newnham College, Cambridge.

Introduction.

The experiments described in this Report were for the most part begun in 1897, and are still in progress. A part of the cost of the work has been defrayed from the Government Grant Fund, the sums thus received having been in part allotted to us by the Evolution Committee, and in part directly by the Grant Committee. The use of the garden in which the botanical experiments were carried out was kindly permitted during 1901, rent free, by the Botanic Garden Syndicate.

Following recognition of the fact that variations of animals and plants may be distinct phenomena, according as they are continuous or discontinuous, it seemed desirable to ascertain in as many cases as possible which variations belong to each of these categories. To answer this question specifically with regard to a diversity of forms, taking each character separately, and testing it by direct experiment in cross-breeding, was a primary object of our work. Such determinations must, in our judgment, constitute a first step in attempting to proceed with the problem of the nature and origin of Species.

Moreover, from what had been hitherto ascertained regarding the phenomena of heredity, the inference could scarcely be avoided that no universal law obtains, but that by studying various specific cases distinct specific laws may be detected.

Another object we have kept in view, is to test the possibility that in-breeding may have a specific effect in modifying the power of transmitting parental character to offspring. There are some indications,*

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* The most remarkable illustration of this phenomenon is that which is alleged

derived from various sources, which point to such a possibility, and tend to show that an in-bred individual of a given breed A, when crossed with an individual of a different breed B, will be more likely to "transmit" the A characters to the offspring—in ordinary terms more "prepotent"—than another individual of the same breed A which was not in-bred, though equally pure or "thoroughbred." It did not appear that this possibility had been properly investigated by scientific methods, though otherwise expressed it is not unfamiliar to practical breeders. For example it is commonly believed that, *cæteris paribus*, a thoroughbred animal is more likely to stamp its own character on its offspring than an animal which is not a thoroughbred.

Thoroughbred animals are not rarely in-bred, and the possibility that the prepotency may be due to the in-breeding rather than the pure-breeding should be borne in mind. It is needless to emphasise the great practical and scientific consequences of such a proposition if it could be established.

Five years ago nothing could have seemed simpler, practical difficulties apart, than to investigate this question and to put it to an experimental test.* Meanwhile, however, as will presently appear, the whole problem of heredity has undergone a complete revolution, and the old idea of prepotency, if it is to be retained at all, must be otherwise conceived. Evidence of greater or less prepotency obtained by

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on the experience of breeders of so-called "light mules" between the canary and the goldfinch. Goldfinch mules are almost invariably bred between the canary hen and the cock goldfinch, for it is only exceptionally that the hen goldfinch breeds in captivity. It is stated that, in the vast majority of cases, the result of such mating is a "dark" mule, resembling the goldfinch in general colour. Very rarely the mule is light, *i.e.*, showing a good deal of the colour of the canary. At the cage-bird shows special classes and prizes are provided for such "light" mules, which are keenly sought for. It is stated by numerous writers on the subject that the probability of breeding "light" mules is greatly increased by using for the mother an in-bred—or, as is known in the fancy, a "sib-bred"—canary hen. This statement was, I understand, first publicly made by Mr. R. L. Wallace, the author of 'The Canary Book,' who there discusses the doctrine at length. However the truth may be, it is undoubtedly widely believed by mule-breeders, with the result that birds which are authenticated as "sib-bred" command an increased price. It is also asserted that since the promulgation of this theory light mules have become much commoner than they used to be. The possibility, however, should not be forgotten that the prepotency of the sib-bred hens *may* have been an original character of their particular strain, and we do not know any experimental *proof* that this prepotency has been brought about by consanguineous mating, though we think the latter hypothesis likely. [For further discussion, see p. 156.]

* Whether in-breeding between brother and sister as pursued in the poultry experiments has led to decline in fertility and weakness of constitution, is not really clear. We hope to publish details of experiences on this question when more material for comparison has been acquired. Such decline has been evident in some of the strains, but it is impossible to know how much of this is to be attributed to breeding from pullets before they are fully matured, or in some cases to late hatching.

methods formerly supposed satisfactory is now capable of different interpretations, and it is clear that to obtain a definite result on this point, a new set of precautions must be used. Consequently though some of the evidence to be adduced bears on the question of differential prepotency, we can offer as yet no plain answer to the original question, and some time must elapse before the matter can be definitely determined.

We expected, then, in chosen cases to determine the degree to which certain characters are discontinuous, whether they are capable of blending with their contraries or not, and to what degree their distinctness is maintained on crossing. In suitable cases we hoped further to determine specific laws of heredity, and to ascertain whether these laws can be affected by in-breeding the parental forms. It has always appeared to us that it can only be by *exhaustive study of special cases* that success can be attained in this direction, and that no results are as yet to be expected from partial experiment with a multitude of forms.

Upon these original objects and on several collateral subjects our experiments have given information. They are still, however, in the initial stage, and we hope to continue them in future years. We greatly regret that from want of space and appliances, we have been obliged to reduce the scope of our experiments to the barest limits. Investigations of this kind to be properly pursued—with animals at least—require far greater resources than we are able to command.

For many reasons we would rather have deferred publication until the work was further advanced, but we feel that with the re-discovery and confirmation of the principle which will henceforth be known as Mendel's Law, the study of heredity and the cognate problems of evolution must enter on a new phase.

At the present time the question how far Mendel's Law with its numerous corollaries is valid, to what cases and to what extent it is of general applicability, supersedes all others in significance. Consequently, our experience, however imperfect, since it bears directly on this question, has a value at this juncture, and we think it may be of use to the many investigators who will doubtless now turn their attention to the experimental study of heredity.

In the history of evolution it must ever be an astonishing fact that Mendel's discovery has so long remained unknown. The obscurity of the Brünn journal is a circumstance quite insufficient to explain the neglect of such a work.* No careful reader could doubt for a moment

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* "Abh. naturf. Ver. Brünn," 1865, vol. 4, p. 1. The author of this remarkable paper, Gregor Johann Mendel, according to a communication made to Correns by Dr. von Schanz, was born in 1822 at Heinzendorf-bei-Odrau in Austrian Silesia. His parents were well-to-do peasants. In 1843 he entered the Königinkloster, an Augustinian house in Altbrünn and was ordained priest in 1847. From 1851–1853 he studied physics and natural sciences at Vienna. On retiring to his cloister he became a teacher in the Realschule of Brünn and afterwards Abbot. He died in

that he was in presence of true facts of exceptional significance. The reason may be that at the time of Mendel's publication, the announcement of the principle of Natural Selection had almost completely distracted the minds of naturalists from the *practical* study of evolution. The labours of the hybridists were believed to have led to confusion and inconsistency, and no one heeded them any more.

It is, perhaps, even more surprising that other investigators failed to discover the same law. Naudin's conclusions came very near it.

The literature of breeding teems with facts now palpably Mendelian. Gärtner, Godron, Laxton, even Darwin himself, must have been many times on the brink of the discovery.

Looking now at such experiments as those of Rimpau with wheat, &c., of Laxton with *Pisum*, Godron with *Datura*, of Darwin with Antirrhinum and sweet peas, we can hardly understand how the conclusion was missed. In Darwin's case no doubt the theory of Pangenesis contributed to difficulty, but some part of the obscurity must have been due to the habit of regarding various species, breeds, varieties, and casual fluctuations as all comparable expressions of one phenomenon, similar in kind; and to insufficient recognition of the possibility that variation may be, in its essence, specific. We may, perhaps, attribute to this preconception the extraordinary complexity with which his experiments on poultry and pigeons were arranged. Various breeds and various crosses were mixed together, and the results are not unlike those which the early chemists would have arrived at in testing the affinities and constitution of a number of unknown elementary and compound substances mixed together at random.

Mendel's Law.

In order to understand what follows it is absolutely necessary that the reader should have a general acquaintance with the present state of knowledge in regard to the Mendelian principle. The original paper is not easily accessible, but it has been reprinted in 'Flora,' 1901, and is about to appear in Ostwald's 'Klassiker der exakten Wissenschaften.' An English translation was published in the 'Journ. Roy. Hortic. Soc.,' 1901. We venture, however, to give a brief outline of the history and progress of the discovery, which is the more necessary

1884. His experiments were made in the garden of his cloister. Besides this paper he published a brief account of experiments with *Hieracium* in the same Journal, vol. 8, 1869, p. 26, and also various observations of a meteorological character. In 1853 and 1854 he published brief notes on *Scopolia margaritalis* and *Bruchus pisi* in the 'Verh. zool. bot. Ver. Wien,' but apparently no others dealing with natural history. Professor Correns informed us that he is said to have spent the later years of his life in the Ultramontane controversy. The Brünn Society, in 1865, was exchanging publications with most of the Academies of Europe, including the Royal and Linnean Societies.

as our own views and modes of expression do not agree wholly with those of other writers on the subject.

It may be premised that the first publication of the re-discovery was made in 1900 by de Vries,* and almost simultaneously by Correns† and Tschermak.‡ There can be no doubt that the appearance of this group of papers constitutes at length a definite advance both in the general study of the physiology of reproduction and in the particular problem of the nature of Species.

In 1865 Gregor Mendel published his discovery. His experiments are described in considerable detail, and the resulting law is stated with emphasis and precision. He at once perceived and lucidly enunciated what he regarded as the essential truth underlying the observed facts. A reader of this paper can hardly fail to recognise its masterly quality. By some strange chance it was ignored, and excepting a casual reference in Focke's 'Pflanzen-Mischlinge' (p. 110) there appears to be no allusion in literature to this remarkable performance. It is a fortunate circumstance that we need feel no hesitation in now accepting Mendel's account; for even if the original paper were such as to admit of doubt, the re-discovery comes to us with a large body of fresh evidence, the simultaneous work of three independent observers, confirming Mendel on the main points.

Mendel states that, like other investigators, he had been struck by the regularity with which offspring of certain hybrids reproduce the pure ancestral forms. But owing, as he supposes, to the complex nature of the cases studied and to want of accurate statistics, the precise facts had never been ascertained. Accordingly he set himself to work out some case from which every confusing element should as far as possible be excluded. After several trials he chose the varieties of *Pisum sativum* as best suited to his purpose. Besides other advantages, this species is well known to have the exceptional merit of being habitually self-fertilised, in N. Europe at least. From the many varieties of peas he first chose pairs of varieties, for crossing, in such a way that the members of each pair differed from each other in respect of one definite character. Of such pairs of characters he chose seven, namely: 1. Shape of seed, whether rounded *or* irregularly angular and deeply wrinkled. 2. Colour of cotyledons [" *endosperm*"], whether some shade of yellow *or* green. 3. Colour of seed-skin, whether a brownish shade *or* white (in correlation with white flowers). 4. Shape of ripe pod, whether simply inflated *or* deeply constricted between the seeds. 5. Colour of unripe pod, whether a shade of green *or* bright yellow. 6. Position of flowers,

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* De Vries, 'Comptes Rendus,' March 26, 1900, and 'Ber. deut. Bot. Ges.,' xviii, 1900, p. 83; *ibid.*, p. 435; 'Rev. gén. Bot.,' 1900, p. 257.

† Correns, 'Ber. deut. Bot. Ges.,' xviii, 1900, p. 158; 'Bot. Ztg.,' 1900, p. 232.

‡ Tschermak, 'Ztschr. f. d. landw. Versuchswesen in Oesterr.,' 1900, 3, p. 465.

whether distributed along the stem *or* crowded near the top in a false umbel. 7. Length of stem, whether about 6—7 feet *or* about $\frac{3}{4}$—$1\frac{1}{2}$ feet. Between these various pairs of varieties crosses were then made, the female parent being emasculated.

As to the first two characters the result of the experiment is seen as soon as the cross-bred seeds are ripe; but to study the other five characters it is of course necessary to plant the seeds and grow the plants to maturity. On such examination it was found that in the case of each pair of characters one only was manifested in every cross-bred individual, to the total, or almost total, exclusion of the opposite character. The character which thus prevails is, in Mendel's terminology, the *dominant* (D), the character which is suppressed, being *recessive* (R). In the above enumeration of characters the dominant is placed first in each pair. Reciprocal crosses gave identical results. Briefly, then, D × R or R × D gave offspring which in appearance are all practically D.

The next generation is obtained by allowing the cross-bred plants DR to fertilise themselves. The result of such self-fertilisation is, according to Mendel, that the next generation instead of being uniform like their parents, breaks up into the two original forms. This takes place in such a way that there are on the average *three dominants to one recessive.*

The recessives are thenceforth not only apparently but *actually pure*, and if allowed to fertilise themselves give rise to recessives only, for any number of generations.

The dominants, on the contrary, though they may look alike, can, if allowed to fertilise themselves, be shown to consist of (*a*) individuals which are *pure* dominants, and on self-fertilisation give rise to dominants only; and (*b*) individuals which are cross-breds, and give rise on self-fertilisation to a mixture of dominants and recessives, *again in the proportion of three to one as before.* The *pure* dominants (*a*) are to the cross-bred dominants (*b*) as *one to two.*

The whole result, therefore, of self-fertilising the cross-breds is really 1DD : 2DR : 1RR, though apparently the proportion is 3D : 1R, because DR plants are not to the eye distinguishable from pure D.* The mixed offspring obtained by self-fertilising DR plants of this second generation consist again of D, DR, and R in the same proportions, and so on at each succeeding generation.

Mendel worked with considerable numbers, and it is impossible to doubt the general accuracy of his conclusions. In the case of some of the pairs of characters (notably the 5th) the evidence is much less clear than in the case of others, and it seems possible that in such cases unascertained disturbances may be at work; but on the whole

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* The attempt made by de Vries to indicate this result by an algebraical expression appears to us open to objection, and we prefer the simpler notation of Mendel.

the results, *as average results*, are clear. The purity of the pure dominants and pure recessives resulting from the self-fertilisation of the cross-breds was tested in the case of characters 1 and 2 to the sixth generation, for characters 3 and 7 to the fifth generation, and for characters 4, 5, and 6 to the fourth generation.

Mendel interprets his facts as follows:—They point to the conclusion that in the cross-bred each of its pollen-grains and each of its egg-cells is *either pure dominant or pure recessive*,* *and that on the average there are equal numbers of each kind for each sex.* If the assortment of pollen-grains and egg-cells is then supposed to take place at random, the most probable percentage result is 25D ♀ × D ♂, 25D ♀ × R ♂, 25R ♀ × D ♂, and 25R ♀ × R ♂. As D × R does not differ from R × D, we have therefore 25D : 50DR : 25R. But as cross-breds resemble dominants in appearance, the *apparent* result is 3D : 1R at each successive self-fertilisation of cross-breds.

Mendel next proceeded to cross pairs of varieties differing in respect of *two* characters; for example, a variety having seeds round and yellow with a variety having seeds angular and green; and also pairs of varieties differing in *three* characters; for example, a variety characterised by seeds round, yellow, and in grey-brown skins with a variety having seeds angular, green, and in white skins. The numerical results of these experiments are set out at length, and are too long to repeat. Briefly the result in all cases was that the dominant characters alone appeared in the first cross. When these were self-fertilised, in the case of *two* differentiating characters, *four* different kinds of seeds resulted, namely, round yellow, angular yellow, round green, and angular green. In the case of *three* differentiating characters these were similarly combined in the *eight* possible combinations. In both sets of experiments the numbers of individuals and their constitution, as tested by the seeds they were capable of producing on self-fertilisation, were consistent with the hypothesis arrived at in the case of varieties differing in respect of one character, namely, that each male and female cell of the cross-bred is pure in respect of one character of each pair of characters, and is capable of transmitting this character to the exclusion of the opposite character; that the reproductive cells are, in the cross-breds, of as many kinds as there are possible combinations of pure characters (taken two or three together, as the case may be); and, finally, that each kind is represented in the cross-breds on the average in equal numbers.

Mendel next tested the truth of the hypothesis that both male and female cells were similarly differentiated, by crossing the first crosses with pure D and pure R forms respectively, finding, as he expected, that DR × D gives the ratio 1DD : 1DR, and that DR × R gives on

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* In what follows such forms are spoken of as "extracted" dominants, or "extracted" recessives.

the average the ratio 1DR : 1RR. Both sets of germ-cells are therefore similarly differentiated.*

It must be understood that this condensed statement does no justice to the lucidity and completeness of Mendel's account of his facts, and of the reasoning based on them. With regard to the numbers, it may be said that though there is a good deal of irregularity, yet taken together they plainly bear out the law as a statement of average results.

De Vries† working with pairs of varieties belonging to a diversity of genera and species, found that in a large number of cases one of the varietal characters was definitely dominant, prevailing in the first crosses to the exclusion of the recessive character. In several of these cases the offspring of the cross-breds fertilised *inter se* were mixed dominants and recessives in proportions fairly agreeing with Mendel's law. In the case of two colour varieties of *Papaver somniferum*, the constitution of the resulting dominants was investigated, and shown to be also according to the law. In certain cases also the purity of the recessives was tested and found to be complete.

De Vries' first announcement was followed almost immediately by the appearance of a paper by Correns,‡ giving an account of some years' work with peas, repeating Mendel's experiments and confirming them as regards the colour of the seeds.

Correns stated that he has tested the purity of the pure dominants and pure recessives to the third generation, and he has kindly informed us that a fourth generation is equally pure.

In addition to these, Tschermak has given an account§ of simultaneous investigations also carried out on varieties of peas. This last paper is an elaborate memoir giving in addition valuable information on several points not directly relating to the present subject.

Tschermak worked with many varieties of peas, and though he obtained several results not wholly consistent with Mendel's law, and some actually conflicting evidence, the general tenour of his work is confirmatory. He gives, in particular, results as to the crossing of cross-breds with one or other of the pure forms.

It is an obvious corollary from Mendel's law that the cross-bred crossed with the recessive parent should give seeds of the dominant and recessive colours in equal numbers. On the other hand, the cross-bred crossed with the dominant should give dominants only (of which half should be pure and half cross-bred in composition). Tschermak's numbers though insufficient for a thorough test, are in fair harmony

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* As it happens, almost all our breedings of cross-breds with pure types have been in the form cross-bred ♀ × pure ♂, but reciprocal experiments are in progress.

† C.R., 1900, March 26; 'Ber. deut. Bot. Ges.,' 18, 1900, p. 83.

‡ 'Ber. deut. Bot. Ges.,' 18, 1900, p. 158.

§ 'Ztsch. f. d. landw. Versuchswesen in Oesterr.,' 3, 1900, p. 465; continued later, *ibid.*, 4, 1901, p. 641, and 'Ber. deut. Bot. Ges.,' 19, 1901, p. 35.

with Mendel's hypothesis. He believes also that there is evidence that yellow is more decidedly dominant over green than the rounded character is over the wrinkled, and on this point further experiments are required.

Subsequently a paper by Correns* has appeared describing his experiments with a glabrous and a hoary form of garden stock (*Matthiola incana*), and giving results as to these varieties, tested by self-fertilisation, and also by recrossing the cross-breds with the parental forms. In this, as in each of the other papers, there are many points which call for separate notice and discussion, but the facts taken together are in fairly close agreement with the expectation given by Mendel's law, though the discrepancies are decidedly greater in this case than in the others. The case happens to be one which had also formed a subject of our experiments, and the various questions raised by the facts will be discussed in connection with the statement of our results.

Lastly, Professor Correns has also published† an elaborate and important memoir on the results obtained in crossing varieties of maize. Some of these results are of a complex character, but the essential fact of the truth of Mendel's law in its application to many of these cases was fully established. From the striking differences between these varieties in several characters, notably in the constitution of the endosperm, whether round starchy (dominant) or wrinkled and sugar-containing (recessive), this case is a most attractive subject for such experiments.

In the characters of the endosperm in maize de Vries‡ also demonstrated the truth of Mendel's law. As regards the colour varieties, Correns showed many complications to exist owing to the fact that the general appearance of the seed depends partly on maternal and partly on embryonic elements; and in some of the characteristics there are other confusing factors owing to fluctuations in the intensity of the dominance.

The above is a brief sketch of a vast mass of observations all tending to the same conclusion, and the truth of the law enunciated by Mendel is now established for a large number of cases of most dissimilar characters, beyond question.

Let us now shortly distinguish what is essential in the new discovery from what is not. The fact that in the cross-bred one character, in appearance, dominated to the exclusion of the other is not of the essence of Mendel's discovery. Tschermak, for instance, saw some exceptions to this rule in *Pisum*. Among the *Matthiola* crosses here

* 'Bot. Cblt.,' 1900, 43, p. 97.

† 'Biblioth. Bot.,' 1901, Heft 53.

‡ 'Rev. gén. Bot.,' 12, 1900, p. 270.

described, and among those originally made by Trevor Clarke,[*] the hoary form *seems* to be not exclusively dominant. Correns saw considerable fluctuations in the dominance of the colours of maize. It is practically certain some of the poultry cases about to be described exhibit the same phenomenon. In fact, generally speaking, there are good reasons for thinking that in numerous instances purity of gametes may occur without either character exhibiting dominance.

There is also some reason for supposing that alterations in dominance may be affected by changes in conditions (see p. 136), and possibly even by differences in the state of the parents, though the only considerable body of evidence relating to these points, obtained by Vernon[†] in Echinid crossing, still needs repetition and confirmation.

The essential part of the discovery is the evidence that *the germ-cells or gametes produced by cross-bred organisms may in respect of given characters be of the pure parental types and consequently incapable of transmitting the opposite character:* that when such pure similar gametes of opposite sexes are united together in fertilisation, the individuals so formed and their posterity are free from all taint of the cross; *that there may be, in short, perfect or almost perfect discontinuity between these germs in respect of one of each pair of opposite characters.*

Doubt might naturally be felt as to the acceptance of a proposition so far-reaching, but it is impossible to see any other possible interpretation of the facts. The pure dominant and pure recessive members of each generation are not merely like, but identical with the pure parents,[‡] and their descendants obtained by self-fertilisation are similarly pure. If they are pure, surely the male and female elements of which they were composed must also be pure.

In another part of this Report we propose to discuss the bearing of these remarkable facts, and to show some of the conclusions to which they point. It will be seen that they provide satisfactory interpretations of some of those redoubtable paradoxes which have hitherto been so mysterious to all evolutionists.

We may now proceed to the description of our own experiments.

LEPIDOPTERA.

In addition to the work here described experiments were made in crossing *Pieris napi* with the var. *bryoniæ*, and *Pararge egeria* with the var. *egerides.* These crosses were pursued for some years until the strains were exterminated by disease.

The results are not altogether consistent, and in the case of *Pieris*

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[*] 'Rep. Intern. Hort. Exhib. and Bot. Congr.,' 1866, p. 142. As the sequel will show, this appearance is otherwise explicable.

[†] Vernon, H. M., 'Phil. Trans.,' B, 1898, vol. 164, p. 465.

[‡] Correns, in maize, has found an apparent change in the degree of dominance of certain characters in the "extracted" variety.

napi are highly complex. In the light of present knowledge we desire to repeat these experiments, and we hope to clear up some of the difficulties before publishing. To those who have leisure for such work, we suggest these species as offering unusually good opportunities for investigating problems of heredity, and we should be glad to communicate with any one who cares to undertake such work.

PART I.—EXPERIMENTS WITH PLANTS, CARRIED OUT BY E. R. SAUNDERS.

Choice of Subjects for Experiment.

In "The Variation of Animals and Plants under Domestication,"* Darwin mentions among other instances of plants in which the absence of blending of the parental characters in the offspring is well-marked, the case of certain hoary and glabrous varieties of garden stocks; when these varieties were intercrossed the foliage of the offspring resembled one or other of the two parents, and intermediates did not occur. The evidence upon which this statement rests is furnished by the experiments of Trevor Clarke, a brief reference to which is found in the 'Gardener's Chronicle,'† and a fuller statement in the Report of the Proceedings of the International Horticultural Exhibition and Botanical Congress, held in London in 1866.‡

In these experiments the "little annual glabrous-leaved stock of the nurserymen" was crossed with pollen from a large hoary biennial form (*Cocardeau* of the French); the result was that one half of the seedlings were glabrous or "Wall-flower leaved," and the other half rough like the male parent—none were intermediate in leaf character.

The glabrous seedlings were, however, no longer dwarf but "of tall and strong habit." The author further states that succeeding generations raised from the hoary cross-breds produced a percentage of glabrous plants, but that the converse was not observed and probably did not occur. Moreover these experiments were verified by repeated trials, which were followed in every case with the same result. Similar results were obtained from intercrossing races which differed in seed colour, as *e.g.*, a purple flowered Queen stock with black seeds, and a red flowered stock with brown seeds. These statements suggested that the stock would afford excellent material for statistical experiments upon cross-breeding. The choice of this genus has, moreover, the following advantages: the plants are hardy and flower freely; the flowers are fairly easy to handle; self-fertilisation occurs in the course of nature, so that a succession of generations, thus raised, can be obtained without other treatment than that of covering the flowers; the seeds

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* Ed. 2, vol. 2, p. 71.

† 1866, p. 588.

‡ p. 143.

germinate readily and they are easily harvested, since the fruits can be gathered before they dehisce.

As a like case of complete discontinuity in the character of the leaf surface had also been observed by de Vries in the case of *Lychnis vespertina* and its glabrous variety, a parallel set of experiments was therefore carried out with the hoary forms *vespertina* and *diurna*, and white and red flowered glabrous varieties. All the forms are diœcious, and thus possess a two-fold advantage, there is no question of emasculation, and consequently no possibility of accidental self-fertilisation through faulty manipulation.

In addition to the above, two other genera were selected for experiment, viz., *Atropa Belladonna* type form and var. *lutea*, both of which at the time were available in the Cambridge Botanic Garden, and *Datura Stramonium* and *D. Tatula*, of which the prickly and smooth fruited forms have appeared to more than one of the earlier workers on hybridisation to be favourable subjects for investigation.*

These experiments were begun in 1897; in 1900 de Vries published the papers† in which he draws attention to the results obtained by Mendel, and enumerates various cases in which he finds that Mendel's law holds, including among them *Lychnis vespertina* type form and var. *glabra*, and *Datura Tatula* and *Stramonium*. Later in the same year Correns‡ published an account of his experiments upon *Matthiola*, showing to what extent Mendel's law applies in the particular races of stocks which he employed. In addition to the work of these observers it seems desirable at this point to give a full statement of the statistical results obtained in our experiments, especially as in the case of Matthiola they have revealed more complex issues than appear in the simple case examined by Correns.

Throughout these experiments the flowers to be fertilised were emasculated (when hermaphrodite), and covered before the dehiscence of the anthers and the unfolding of the corolla, while the pollen was usually taken from covered flowers, or from buds picked while still unopened; in the case of some hoary strains of stocks growing alone or at a distance from those under experiment, this latter precaution was considered unnecessary. In both Atropa and Datura the habit of the plant and the disposition of the flowers render it easy to place the buds expanding simultaneously on any individual under separate covers, an arrangement which minimises the possibilities of error; to have attempted to secure similar conditions in Matthiola, in which the flowers are closely crowded and open in rapid succession, would have involved an expenditure of labour, or a sacrifice of material which would not

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* Koelreuter, Gaertner, Naudin, Godron. For the literature see Focke, 'Die Pflanzen-Mischlinge,' 1881, p. 263.

† 'Comptes Rendus,' March 26, 1900, and 'Ber. Deut. Bot. Gesell.,' Bd. 18, 1900, p. 83.

‡ 'Bot. Centralblatt,' Bd. 84, 1900.

have been possible without seriously reducing the number of experiments: except in special cases therefore, it was not attempted.

Preliminary Statement of Results.—It may be stated at once that the phenomena in Lychnis, Atropa, and Datura follow Mendel's law with considerable accuracy, and no exceptions that do not appear to be merely fortuitous were discovered.

In the case of Matthiola, the phenomena are much more complex. There are simple cases which follow Mendelian principles, but others of various kinds which apparently do not. The latter cases fall into fairly definite groups but their nature is still obscure.

In the following pages it will be convenient to deal with the simpler cases first.

LYCHNIS.

The two forms *L. vespertina* and *L. diurna* were each intercrossed with white-flowered and red-flowered glabrous varieties. *L. vespertina* is a native of Cambridgeshire, and wild plants were therefore easily procured in the neighbourhood; *L. diurna* is not found in the county, and seeds of this form were collected in Cornwall. For the glabrous varieties, which were at the time growing in the Cambridge Botanic Garden, we are specially indebted to Professor de Vries.* All the forms are perennial.

The discontinuity between the hairy and the glabrous forms appears to be absolute; among the whole number of plants raised, not a single intermediate was observed. Such, however, is not the case when characters other than leaf surface are considered, as *e.g.*, colour of corolla (white or red), position of capsule teeth (erect or recurved), colour of seed (grey or black). When a cross was made between the types differing in respect of these latter characters, the offspring exhibited a series of intermediate forms. The corolla varied from the deep red of *diurna* to the palest pink, but was rarely, if ever, pure white; the capsule teeth might be directed obliquely upwards, as in *vespertina*, or be turned downwards and slightly recurved, or be in any intermediate position; but the rolled form characteristic of *diurna* was extremely rare. The seeds were of all tints from yellowish-grey to black.†

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* The discovery by de Vries of a wild specimen of *L. vespertina*, var. *glabra*, and the artificial production from it of a smooth red-flowered form are described in his 'Erfelijke Monstrositeiten," p. 10 (p. 26 of the French translation); he names this red-flowered form *L. diurna*, var. *glabra*. It may be noted, however, that such plants grown at Cambridge from his seed, although resembling *diurna* in the colour of the corolla, had not the recurved teeth characteristic of the capsule in that form; on the contrary, they were in this respect similar to the white-flowered form (*L. vespertina*, var. *glabra*) from which they were originally descended. The characters of hairiness and of the capsule-teeth are therefore dissociable.

† For a detailed description of hybrids of *L. diurna* and *L. vespertina* see Gagnepain, 'Bull. de la Soc. Bot. de France,' 1897, Tomes 43 and 44.

The results as regards hairiness are tabulated in the succeeding pages, in which the different forms are briefly indicated as follows:—

WH = *L. vespertina*, plant hairy, flowers white.
RH = *L. diurna*, plant hairy, flowers red.
WG = Glabrous variety with white flowers.
RG = ,, ,, ,, red ,,

In all cases the cotyledons are glabrous, but the seedlings can be sorted as soon as the next pair of leaves appear. In the glabrous varieties no hairs were observed upon any part of the plants at any time.

Table I.—First Cross-bred Generation obtained by crossing the Hairy and Glabrous Forms in each of the eight possible ways.

Parentage.*	Number of seed parents.	Number of flowers.	Number of offspring.	
			Hairy.	Glabrous.
WG × WH........	5	6	91	
WG × RH........	2	3	63	
RG × RH........	4	6	133	
RG × WH........	1	4	126	
WH × WG........	4	12	100	
WH × RG........	1	1	3	
RH × RG........	3	11	208	
RH × WG........	2	9	282	
Total...........	Individuals used more than once.	52	1006	0

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* Throughout the paper expressions in the form A × B indicate that A is the seed parent and B the pollen parent.

Table II.—Offspring of Cross-breds when fertilised *inter se*.*

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.		Totals for each particular kind of union.	
			Hairy.	Glabrous.	Hairy.	Glabrous.
(RH × RG) × (RH × RG)	1	2	17	6	99	27
	1	1	82	21		
(RH × WG) × (RH × WG).............	1	1	31	12	42	16
	1	1	11	4		
(RG × RH) × (RG × RH)..............	1	2	47	17	137	41
	1	1	62	14		
	1	2	28	10		
(RG × WH) × (RG × WH)	1	1	59	14	59	14
(WG × WH) × (WG × WH).............	1	1	15	6	59	24
	1	2	37	16		
			7	2		
(WG × RH) × (WG × RH)..............	1	1	12	4	12	4
Total	..	..	..	..	408	126
Expected result, 3 : 1; actual result, 3·2 : 1						

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* As all the forms employed are diœcious, fertilisation of the cross-breds *inter se* is necessary where the alternative of self-fertilisation would be possible with hermaphrodite types.

Table III.—Offspring of Cross-breds when crossed with the original Recessive (Glabrous) Form.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.		Totals for each particular kind of union.	
			Hairy.	Glabrous.	Hairy.	Glabrous.
(WH × WG) × WG	1	1	31	27	220	211
	1	1	67	60		
	1	2	77	75		
	1	2	45	49		
(WG × WH) × WG	1	2	18	25	18	25
(RH × RG) × RG	1	1	4	4	110	95
	1	2	16	11		
	1	3	90	80		
(RH × WG) × WG	1	1	9	7	39	42
	1	3	7	5		
	1	2	14	24		
			9	6		
(RG × RH) × RG	1	2	13	16	60	60
	1	3	47	44		
Total	..	..	..	..	447	433
Expected result, 1 : 1; actual result, 1·0 : 1.						

Table IV.—Offspring of Cross-breds when crossed with the original Dominant (Hairy) Form.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.	
			Hairy.	Glabrous.
(RG × RH) × RH	1	1	35	
(RH × RG) × RH	1	1	6	
Total	2	2	41	0

Table V.—Offspring obtained by fertilising the Offspring of the Cross-breds *inter se*, (α) when both the final parents are hairy.
(β) ,, ,, ,, ,, glabrous.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.	
			Hairy.	Glabrous.
(*a*.)				
[(WG × WH) × WG] × [(WG × WH) × WG]	1	1	23	6
[(RG × RH) × RG] × [(RG × RH) × RG]	1	1	87	25
Total	2	2	110	31
Ratio			3·5 : 1	
(β.)				
[(WG × WH) × WG] × [(WG × WH) × WG]	1	2		43
[(RG × RH) × RG] × [(RG × RH) × RG]	1	1		8
Total	2	2	0	51

A glance at the preceding tables will show—

(1) That the hairy character is dominant and the glabrous recessive (Table I). Of the thousand cross-breds raised from various unions between hairy and glabrous strains, all, without exception, were hairy.

(2) That such cross-breds invariably yielded both dominant and recessive forms if fertilised *inter se* (Table II), or if crossed with the recessive form (Table III); in the former case in the proportion of (about) 3 D to 1 R, in the latter of 1 D to 1 R; but that when crossed with the dominant form the offspring are again all dominant (Table IV).

(3) That when the offspring of cross-breds were intercrossed, like with like, the result varied according as they were of dominant or recessive form. Recessives fertilised *inter se* yielded only recessives (Table V*b*), but dominants (two individuals) similarly fertilised, yielded dominants and recessives in the ratio 3·5 : 1, thus proving impure dominants (dominant hybrids) which yield both forms in the succeeding generation; had either parent in either case been a pure dominant, the offspring would presumably have been all dominant (see Table IV).

These results clearly show that in the above-mentioned forms of Lychnis we have excellent illustration of a case to which Mendel's law is wholly applicable as regards the particular character of leaf surface.

ATROPA.

I. *First Cross-bred Generation.*

Reciprocal crosses were made between two individuals of *A. Belladonna typica* (flowers brown, fruits black, stem tinged with red = B), and a vigorous specimen of *A. Belladonna*, var. *lutea* (flowers and fruits yellow, stem pure green = Y).* Both forms are perennial.

From crosses of the form B × Y 100 plants were raised, and from the reciprocal unions Y × B, 236. In both sets of cross-breds the fruits (numbering in the three years, during which the plants have been under observation, some thousands) were all black, and though the flowers showed several shades of brown they never varied to pure yellow. The stems were more or less deeply tinged. It would appear then that the colour of the type form is completely dominant in the fruit of the cross-bred, but that in the corolla and stem the intensity of the dark coloration may be more or less diminished.†

II. *Offspring of Cross-breds.*

Twenty-five flowers on as many cross-breds were self-fertilised, but (in consequence perhaps of self-sterility) set no fruit; offspring were therefore obtained by fertilising the cross-breds with pollen from the parent forms.

(α) *Cross-bred × Dominant.*—Flowers on 21 individuals (20 Y × B and 1 B × Y) were crossed with the dominant form; 220 (197 and 23) plants were raised, and all bore black fruits. As in the first cross-bred generation there was complete dominance of the type colour.

β. *Cross-bred × Recessive.*—Flowers on 38 individuals (22 Y × B and 16 B × Y) were crossed with the recessive form, and the seeds of each plant sown separately. In every case a mixed lot of seedlings was obtained, differing in the colour (green or reddish) of the young stem (hypocotyl). Unfortunately a late frost killed an enormous number of the seedlings, before any attempt had been made to estimate at all accurately the total numbers of the two colours; it had, however, been noted, that up to this time there appeared to be either rough equality or a slight preponderance of the pure green. Of those that survived many perished before flowering, owing to the dryness of the season, so that eventually less than 300 plants lived to bear fruit; of

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* There was no difficulty in manipulating this cross, nevertheless few flowers set fruit; 250 were crossed and only about a dozen set seed. The fruits that were formed had a full complement of seed.

† Hoffmann obtained a similar result with these two forms; he states that cross-breds, whether offspring of typica × lutea or lutea × typica, in the two seasons during which they were observed bore only black fruits. The experiments were not apparently continued beyond the first generation. 'Ber. Oberhessische Gesell. für Natur. u. Heilkunde,' 16, s. 14.

these, all those with green stems bore yellow flowers and fruits, those with reddish stems brown flowers and black fruits, but the latter were more than twice as numerous as the former (197 B, 75 Y). In view of the earlier observation on the seedlings, however, it seems extremely doubtful whether any reliance can be placed upon the final numbers. Although, therefore, all that can be stated with certainty is that there is complete agreement with Mendel's law in so far—(1) that the fruit colour of the type form is completely dominant in the first cross-bred generation, whether the cross be of the form D × R or R × D; and (2) that the offspring resulting from a union between a cross-bred and a pure dominant are all dominant, but that when the cross is made with a pure recessive the offspring are mixed dominant and recessive; nevertheless, the observations made at the time of germination suggest that this agreement would probably prove quantitative as well as qualitative.

DATURA.

The following forms were employed—

1. *D. Stramonium* (stems green, flowers white, fruits prickly).
2. *D. Stramonium*, var. *inermis* (stems green, flowers white, fruits smooth).
3. *D. Tatula* (stems reddish, flowers violet, fruits prickly).
4. *D. Tatula*, var. *inermis* (stems reddish, flowers violet, fruits smooth).

Reciprocal crosses between these different types showed clearly that of the two pairs of antagonistic characters the violet colour is dominant, the white recessive, and similarly that the armed condition is dominant and the unarmed recessive; also that these results obtain whichever combination of forms is employed.

Several earlier observers have selected the various species of Datura as affording suitable material for the study of hybrids. Naudin* crossed *D. Stramonium* with *D. Tatula*, and *D. Tatula* with *D. Stramonium*, and found that in both cases the first generation of cross-breds resembled *D. Tatula*; in the second generation both the parent forms appeared, but *D. Tatula* was more abundant than *D. Stramonium*—the actual figures are not given. Similarly with *D. Stramonium* and *D. lævis*, the first generation resembled *D. Stramonium*, the second produced both forms. Later Godron's† results appeared with a record of the numbers obtained. This observer found that *D. Bertolonii*‡ crossed with *D. Tatula* yielded offspring all resembling *D. Tatula*; but that

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* 'Nouv. Arch. Mus.,' 1, p. 41; for the earlier literature, see Focke's 'Pflanzen-Mischlinge,' p. 263.

† 'Mém. Acad. Stanisl.,' 1864, 1865, 1872.

‡ *D. Bertolonii* of Godron = *D. Stramonium*, var. *inermis*. *D. lævis* of Naudin is a white-flowered unarmed form not very different from this.

among the 29 plants obtained in the second generation three distinct forms occurred, viz., *Tatula*, *Tatula* var. *inermis*, and *Stramonium*, and in the proportion respectively of 16, 11, and 2. It will be noticed that with both observers *Tatula* was found to be a dominant form. As regards Godron's second result, a comparison with the following tables would seem to show that the numbers in the second generation are too small to afford conclusive evidence either as to the possible number of forms which may result from this particular union, or as to the relative abundance of each.

From two other experiments described by Godron it would appear that the offspring of cross-breds *may* exhibit a character which had not (presumably) been introduced by either of the original parents; *e.g.*, *Stramonium* × *Tatula* yielded in the second generation the four forms *Stramonium*, *Bertolonii*, *Tatula*, and *Tatula*, var. *inermis*, although neither of the original parents possessed unarmed fruits. Again from a cross between *Tatula* and *Tatula* var. *inermis*, he obtained in the second generation both the parent forms, and also *Bertolonii*, although both parents were of the dominant colour.

In each case it will be noticed that the unexpected form of offspring belonged to a recessive type. These results are at variance with those detailed below, but in the light of the facts which we now know, a possible explanation of these apparent contradictions at once suggests itself. May it not be that one (or both) of the crossed forms, although apparently pure, was in reality a cross-bred—an impure dominant—exactly resembling the pure dominant type which it was intended to employ? Godron states that the type forms were grown together in the same garden, and that he had been led to conclude that it was not necessary to cover the flowers in order to avoid chance cross-fertilisation. If then it is also borne in mind that a plant which in fruit-form, and in the colour of stem and flower has all the appearance of a specimen of *D. Tatula*, may, nevertheless, when self-fertilised, prove by its mixed offspring that it is not "pure" but a cross-bred derived from a cross with any one of the three forms *Tatula* var. *inermis*, *Stramonium*, or *Stramonium* var. *inermis*; it seems not impossible that such an unsuspected cross-fertilisation may have occurred among Godron's plants; for the effect of such a cross is not immediately apparent—not, in any case, until the next generation but one. These considerations suggest a very necessary precaution in all experiments of this kind, viz., the carrying out of control experiments in order to test the purity of the parent plants. When the immediate parentage of the individuals selected for crossing is unknown, the self-fertilisation of additional flowers would yield valuable evidence in corroboration (or otherwise) of the results obtained by cross-fertilisation. The importance of such controls in cases of complete dominance is obvious. The alternative hypothesis is, of course, that an original variation occurred.

Although the offspring resulting from a cross between any two of the forms employed are usually indistinguishable from the type which is dominant as regards the particular character crossed, yet in other cases the intensity of a dominant character may be more or less diminished either in particular individuals or in particular parts of one individual. In Tatula-Stramonium cross-breds the corolla is often paler in colour than that of the dominant parent (as has already been noticed by Naudin),* but even in the palest specimens the deep blue colour of the unopened anthers leaves no doubt as to the presence of the dominant colour element. When the seedling offspring of these cross-breds are sorted into groups according to the pure green or reddish-green colour of the hypocotyl, it was noticed that the tint in the red-stemmed individuals was not equally pronounced in all cases. The occurrence of intermediate forms was also occasionally noticeable in the fruits. Among the large number of capsules examined, there were some of the mosaic type, in which part of the capsule was prickly and the remainder smooth, while others, suggesting a blend, were more or less prickly all over, but the prickles were much reduced in size, and often formed mere tubercles. These mosaics occurred as rarities both on prickly individuals and on smooth ones still more rarely. Naudin observed the not uncommon occurrence of both these intermediate forms, but Godron† only records a single instance. Such intermediate fruits were most often found towards the end of the flowering season; occasionally, however, the first fruit of all was smaller than the others, and in that case often less prickly also. Increase in height and sterility of the flowers at the lower bifurcations occurred among the cross-breds, but to the slight extent observed by Godron, rather than in the more pronounced degree described by Naudin.

In one cross Godron obtained from *Stramonium* × *Bertolonii* plants all like *Bertolonii*, as stated. Among their offspring three forms appeared, *Stramonium*, *Bertolonii*, and *Tatula inermis.* These results are at variance with ours obtained from the reciprocal cross (*Stramonium inermis* × *armata*). Here the offspring resembled *armata*, and in the next generation only the parent-types *armata* and *inermis* came. Moreover, in no other experiment with these types has a dominant character (whether armed fruits or coloured flowers) appeared among the offspring of recessives. Yet in this one case both results are said to have occurred. Here the use of a DR by mistake for DD would not explain the contradiction, and we must suppose either that this is a true exception, or that error occurred in the experiment or description.

An analysis of the results of the various unions is shown in the following tables, in which the parent forms are indicated by the abbreviations T. ar., T. in., S. ar., S. in.

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* *Loc. cit.*

† *Loc. cit.*

I. *First Cross-bred Generation.*

Table VI.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.			
			T. ar.	T. in.	S. ar.	S. in.
T. ar. × T. in. . .	2	3	28 23 17			
		Total	68	0	0	0
T. in. × T. ar. . .	1	1	28			
		Total	28	0	0	0
S. ar. × T. in. . .	1	1	61			
		Total	61	0	0	0
T. in. × S. ar. . .	1	1	41	1		
		Total	41	1	0	0
S. in × T. ar. . .	3	3	43 20 20			
		Total	83	0	0	0
S. in. × S. ar. . .	7	8		61 53 36 32 18 18 18 2		
		Total	0	238	0	0

The cross T. ar. × S. in. was also made, but for some reason the seeds failed to germinate. From seeds of this cross (kindly sent by Professor de Vries), however, twenty plants were obtained, all resembling the type T. ar.

It will thus be seen that more than 500 cross-breds were obtained from seven different unions between the four type forms, and that, if we except a single plant,* the uniform result is that when armed and

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* This plant bore a single undersized smooth fruit; as no flowers were subsequently produced, further evidence as to the true character of the plant could not be obtained. But in view of the uniformity of the results as regards the complete dominance of the armed character in all other cases, it seems at least possible that a stray pollen-grain or a stray seed may account for this solitary exception.

unarmed races are intercrossed the armed character is dominant, and that when Tatula and Stramonium forms are crossed together the dark colour of the former is also dominant.

II. *Offspring of Cross-breds.*

(α.) When Tatula *or* Stramonium cross-breds are self-fertilised.

Table VII.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. ar. × T. in.) × self	3	3	62		19	1		
			31		18	6		
			30		24	5		
		Total	123	0	61	12	0	0
(T. in. × T. ar.) × self	2	2	49		19	6		
			34		all killed by frost.			
		Total	83	0	19	6	0	0
(S. in. × S. ar.) × self	4	4		54			27	16
				49			34	5
				10			6	2
				8			5	2
		Total	0	121	0	0	72	25

Table VII shows that when cross-breds derived from unions between armed and unarmed races of *like* colour were self-fertilised, the offspring also were of one colour, uniform with that of the parents; but that as regards the fruits, they were in each case divisible into two groups, having respectively the types of capsule characteristic of the two parents. In two sets out of the three the totals approximate very closely to the expected ratio 3D : 1R, though individuals gave wide results; the remaining set, it will be noticed, includes one case in which there is a considerable discrepancy between the theoretical 3 : 1) and the observed (19D, 1R) result. The explanation possibly ies in the fact that more than two-thirds of the seedlings perished, and therefore the final numbers may not represent at all accurately the original proportion of the two forms. If this case be excluded, the agreement is fairly precise.

(β.) When Tatula–Stramonium cross-breds are self-fertilised or fertilised *inter se*.

Table VIII.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. ar. × S. in.) × self or *inter se*	6	6	37	20	17	5	5	2
			18	7	11	4	2	—
			25	9	21	2	6	—
			45	17	33	9	14	—
			28	8	20	6	6	1
			17	12	15	2	9	2
		Total	170	73	117	28	42	5
(S. in. × T. ar.) × self	2	2	266	92	18	16	4	3
			Not recorded.		22	9	14	2
		Total	?	?	40	25	18	5
(T. in. × S. ar.) × self	6	7	58	28	2	1	—	—
			29	11	7	1	2	2
			80	29	14	5	8	1
			60	23	5	1	5	—
			64	19	15	3	4	—
			7	3	4	1	2	—
		Total	298	113	47	12	21	3

In Table VIII we have the corresponding results obtained from cross-breds when the original parents *differed not only in the character of the fruit, but also in colour.* In the first two cases the two dominant and the two recessive characters were distributed in different parents; in the third each parent combined one dominant with one recessive character. On the Mendelian hypothesis we should expect all four forms to result from each of these combinations in the proportion

T. ar. : T. in. : S. ar. : S. in. : : 9 : 3 : 3 : 1 ;

stating the same result in terms of either character (*i.e.*, colour or fruit form) considered alone, we should expect in each case the ratio 3D : 1R. As regards the results actually obtained, it will be seen that they accord with expectation in so far that all four types appeared in each set of unions, and that in every case Tatula plants were more numerous than Stramonium, and armed than unarmed; on the other hand, the total number of Stramonium plants somewhat exceeds that demanded by the theory, while that of the wholly recessive and least frequently occurring form S. in. is considerably below the calculated result. In considering the former discrepancy it should, however, be borne in mind that any errors in the classification of the many seedlings which perished early would all tend in the same direction, viz., to increase the Stramonium totals, since in the youngest seedlings the tinge of red is sometimes so faint that it may occasionally have escaped notice altogether; and regarding the latter, that in many cases the number of Stramonium plants which lived to maturity was decidedly small.

In the results recorded in Tables IX, X, and XI we have a much closer agreement with Mendel's ratio. Many of the cross-bred parents here used were among the number of those employed in the preceding experiments, where the expected result was less consistently approached, but there are manifestly more possibilities of fluctuation in the one case than in the other.

(γ.) When the cross-breds are crossed with the original recessive form

Table IX.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. ar. × T. in.) × T. in.	3	3	56 36 19		23 19 8	24 13 11		
		Total	111	0	50	48		
Expected result	..	..	*All T.*		*1*	*1*		
(T. in. × T. ar.) × T. in.	2	2	45 ∞ (Almost all killed by frost)		6 5	7 —		
		Total	?	0	11	7		
Expected result	..	..	*All T.*		*1*	*1*		
(T. ar. × S. in.) × S. in.	6	6	Not recorded		9 8 6 3 1	10 6 6 3 1	8 6 11 5 —	6 7 6 3 2
		Total			27	26	30	24
Expected result	..	..			*1*	*1*	*1*	*1*

(δ.) When the cross-breds are crossed with the original dominant form.

Table X.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. in. × T. ar.) × T. ar.	1	1	27		23			
Expected result	..	..	*All T.*		*All ar.*			
(S. in. × S. ar.) × S. ar.	1	1		51			34	
Expected result	..	..		*All S.*			*All ar.*	
(S. in. × T. ar.) × T. ar.	1	1	79		29			
Expected result	..	..	*All T.*		*All ar.*			

(ε.) When the cross-breds, whose parents each combined one dominant with one recessive character, are crossed with one of the parent forms.

Table XI.

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.					
			Number of seedlings.		Number of plants which matured fruits.			
			T.	S.	T. ar.	T. in.	S. ar.	S. in.
(T. in. × S. ar.) × S. ar.	3	3	59 103 7	51 108 8	3 9 6		3 7 7	
		Total	169	167	18	0	17	0
Expected result	..	..	*1*	*1*	*All ar.*		*All ar.*	

III. *Subsequent Generations.*

Case 1. Parentage [(T. ar. × S. in.) × Self] × Self.
Assuming that Mendel's law holds,

T. ar. × S. in. gives all T. ar., impure, because

any such cross-bred (T. ar.) × Self gives a mixed offspring in the proportions 9 T. ar., 3 T. in., 3 S. ar., 1 S. in.

But of sixteen such individuals only one of each kind (four in all) is pure, yielding its like and only its like when self-fertilised ; from each of the twelve remaining plants (when self-fertilised) more than one type will be obtained. For

the 9 apparent T. ar. plants represent 4 different kinds of individuals, viz. :—

(*a*) 1 pure T. ar., yielding only T. ar.; indicated by the expression T. ar. (T. ar.).
(*b*) 2 impure T. ar., yielding T. ar. and T. in. in the ratio of 3 : 1; indicated by the expression T. ar. (T. in.).
(*c*) 2 impure T. ar., yielding T. ar. and S. ar. in the ratio of 3 : 1; indicated by the expression T. ar. (S. ar.).
(*d*) 4 impure T. ar., yielding T. ar., T. in., S. ar., S. in., in the ratio of 9 : 3 : 3 : 1 indicated by the expression T. ar. (S. in.).

the 3 apparent T. in. plants represent 2 different kinds of individuals, viz. :—

(*e*) 1 pure T. in., yielding only T. in.; indicated by the expression T. in. (T. in.).
(*f*) 2 impure T. in., yielding T. in. and S. in. in the ratio of 3 : 1; indicated by the expression T. in. (S. in.).

the 3 apparent S. ar. plants represent 2 different kinds of individuals, viz. :—

(*g*) 1 pure S. ar., yielding only S. ar.; indicated by the expression S. ar. (S. ar.).
(*h*) 2 impure S. ar., yielding S. ar. and S. in. in the ratio of 3 : 1; indicated by the expression S. ar. (S. in.).

the 1 S. in. is pure, yielding only S. in., indicated by the expression S. in. (S. in.).

Thus it is obvious that only in the case of those among the offspring of cross-breds (self-fertilised) which exhibit both recessive characters is it possible to know, without further experiment, with exactly what kind of individual one is dealing. In the following experiment a single flower was self-fertilised on each of eight individuals selected at random from among the offspring of cross-breds, viz., 3 T. ar., 4 T. in., and 1 S. ar. The results tabulated below afford a striking illustration of the Mendelian principle.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.				Conclusions.
		T.	S.	T. ar.	T. in.	S. ar.	S. in.	
A	T. ar.	56		17	6			∴ A = T. ar. (T. in.)
B	,,	42	15	32		7		,, B = T. ar. (S. ar.)
C	,,	235	80	11	4	3	2	,, C = T. ar. (S. in.)
D	T. in.	27			10			,, D = T. in. (T. in.)
E	,,	15			4			,, E = T. in. (T. in.) probably
F	,,	23	7		20		5	,, F = T. in. (S. in.)
G	,,	8	2		8		1	,, G = T. in. (S. in.)
H	S. ar.		19			11	6	,, H = S. ar. (S. in.)

Case 2. Parentage [(T. ar. × S. in.) × S. in.] × Self.

In this case we should expect to find that only four kinds of individuals would occur among the offspring of the cross-breds (T. ar. × S. in.) resembling in appearance the four type forms, and therefore that all those of similar appearance would give similar results as follows:—

Any T. ar. would yield a mixed offspring in the proportions 9 T. ar., 3 T. in., 3 S. ar., 1 S. in.; ∴ T. ar. (S. in.).

Any T. in. would yield a mixed offspring in the proportions 3 T. in., 1 S. in.; ∴ T. in. (S. in.).

Any S. ar. would yield a mixed offspring in the proportions 3 S. ar., 1 S. in.; ∴ S. ar. (S. in.).

Any S. in. would yield a pure offspring all S. in.; ∴ S. in. (S. in.).

A single flower was self-fertilised on each of five individuals among the offspring of the cross-breds, viz., 1 T. ar., 1 T. in., 2 S. ar., 1 S. in., and the anticipated result was obtained.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.				Conclusions.
		T.	S.	T. ar.	T. in.	S. ar.	S. in.	
I	(T. ar.)	Many	Few	6	1	5	1	∴ I = T. ar. (S. in.)
J	(T. in.)	71	23		38		19	,, J = T. in. (S. in.)
K	(S. ar)		120			27	10	,, K = S. ar. (S. in.)
L	(S. ar.)		153			34	12	,, L = S. ar. (S. in.)
M	(S. in.)		27				20	,, M = S. in. (S. in.)

Case 3. Parentage [(T. ar. × S. in.) × S. in.] × S. in.

The offspring of any individual (T. ar. × S. in.) × S. in. should in this case exhibit the same number of forms as the offspring of any individual of similar appearance in the preceding experiment, but in the ratio, when mixed, of 1 : 1, instead of 3 : 1. The qualitative result was obtained, and, considering the small totals, the numbers may reasonably be taken to indicate a quantitative agreement also.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.				Conclusions.
		T.	S.	T. ar.	T. in.	S. ar.	S. in.	
L	(S. ar.)		124			23	18	∴ L = S. ar. (S. in.)
N	(S. in.)		115				42	,, N = S. in. (S. in.)
O	(T. ar.)	43	35	15	11	9	18	,, O = T. ar. (S. in.)

Case 4. Parentage [(T. in. × S. ar.) × S. ar.] × Self.

Among the offspring of (T. in. × S. ar.) × S. ar., we find two forms only, viz., T. ar. and S. ar., but we may expect each form to include two kinds of individuals; there would thus be four kinds of individuals in all, of which one alone would be pure, and three impure, viz.,

(1) T. ar. yielding a mixed offspring in the proportions 9 T. ar., 3 T. in., 3 S. ar., 1 S. in.; ∴ T. ar. (S. in.).
(2) T. ar. yielding a mixed offspring in the proportions 1 T. ar., 1 S. ar.; ∴ T. ar. (S. ar.).
(3) S. ar. yielding a mixed offspring in the proportions 1 S. ar., 1 S. in.; ∴ S. ar. (S. in.).
(4) S. ar. yielding a pure offspring all S. ar.; ∴ S. ar. (S. ar.).

The nine individuals selected at random, viz., 4 T. ar. and 5 S. ar. justified expectation.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.				Conclusions.
		T.	S.	T. ar.	T. in.	S. ar.	S. in.	
P	(T. ar.)	72	20	65		18		∴ P = T. ar. (S. ar.)
Q	,,	100	30	45	14	14	5	,, Q = T. ar. (S. in.)
R	,,	43	19	20	7	8	5	,, R = T. ar. (S. in.)
S	,,	58	17	30	7	12	5	,, S = T. ar. (S. in.)
T	(S. ar.)		115			85		,, T = S. ar. (S. ar.)
U	,,		13			10		,, U = S. ar. (S. ar.)
V	,,		22			17		,, V = S. ar. (S. ar.)
W	,,		193			69		,, W = S. ar. (S. ar.)
X	,,		366			204	50	,, X = S. ar. (S. in.)

Case 5. Parentage [(T. in. × S. ar.) × S. ar.] × S. ar.

Five of the individuals used in the preceding experiment, viz., P, Q, R, T, U, were crossed with the pure form S. ar.; from T. U, the offspring would presumably be all S. ar., while from P, Q, and R alike, if the conclusions stated above are correct, we should expect the result 1 T. ar. : 1 S. ar. From each individual a result in accord with the expectation was obtained.

Plant.	Type.	Number of seedlings.		Number of plants which matured fruits.			
		T.	S.	T. ar.	T. in.	S. ar.	S. in.
P	(T. ar.)	68	74	45		52	
Q	(T. ar.)	67	58	40		35	
R	(T. ar.)	49	55	33		36	
	Total ..	184	187				
T	(S. ar.)		110			76	
U	(S. ar.)		69			63	
	Total ..	0	179				

From the various results detailed above we may conclude that, as in Lychnis, and probably also in Atropa, we have obedience to the Mendelian law in the case of a single pair of antagonistic characters, so in Datura we have a similar result for the more complicated case in which two such pairs of characters are concerned.

MATTHIOLA.

Various races of stocks were employed, differing in regard to the character of the leaf-surface, colour of seeds, colour of flowers, and the time of flowering. It was found that the results differed widely according to the variety, and occasionally according to the individual, with which the crosses were made. These differences are highly complex, and in some cases altogether unexpected. After every effort at clearness in arrangement and tabulation, the statement of results remains complicated and difficult to follow.

List of Types used and their Characters.

The various races of stocks* employed differed in regard to

Habit, whether annual or biennial.
Character of leaf surface, whether hoary or glabrous.
Colour of flowers, various.†
Colour of seeds, whether green, brown, or intermediate.

Type 1. Biennial; leaves hoary; flowers white;‡ seeds black in outward appearance, this colour being due to green colour in the embryo overlaid with a violet layer; obtained from a coast-guard station in the Isle of Wight, and probably derived from the wild *M. incana.*

Type 2. Annual; leaves hoary on *under* surface, but glabrous, or nearly so, on the *upper* surface, a condition hereafter called "half-hoary"; flowers white; seeds yellowish brown; from same locality as Type 1. Origin unknown.

Type 3. Annual "ten-week" stocks; leaves hoary; flowers white;

3*a*. Seeds yellowish brown; kindly obtained by Mr. Lynch from the Royal Gardens, Kew.
3*b*. Seeds yellowish brown (commercial seed).
3*c*. Seed colour unknown, plants found in a Cambridge garden.

Of these three forms the first two, 3*a* and 3*b*, were indistinguishable in appearance, but behaved differently in crossing. Of 3*c* very little was known.

Type 4. Annual "ten-week" stock; leaves hoary; flowers purple; seeds green (commercial seed).

Type 5. Annual "ten-week" stocks; leaves glabrous;§

5*a*. Flowers white.		Seeds yellowish brown.
5*b*. ,,	cream or yellowish white.	
5*c*. ,,	red.	
5*d*. ,,	pinkish white.	
5*e*. ,,	bluish pink.	

(Commercial seed.)

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[*] Only single-flowered plants were chosen to breed from in any of these experiments. Doubles constantly presented themselves, but variations in respect of this character were not considered. Records were kept, but are not included in this paper. The same is true regarding the order of flowering of the axes. The character, width of seed-wing, used by Correns, was not studied.

[†] Unfortunately we have not yet fully identified the colour varieties according to the seedsmen's lists. Messrs. Haage and Schmidt have kindly supplied us with a set of their varieties, and from the descriptions and seed-characters we do not doubt that our "cream" is their "sulphur-yellow."

[‡] In 1901 the flowers of this form were faintly tinged with purple.

[§] In these forms the absence of hairs is absolute in many individuals, but in some cases a single hair or group of hairs may occur at the extreme apex of the leaf. The cotyledons of *all* types, whether glabrous or hoary, are invariably glabrous.

Type 6. Annual " ten-week " stocks; leaves glabrous;[‡]

6*a*.	Flowers light purple.	Seeds green.
6*b*.	„ dark purple.	
6*c*.	„ claret coloured.	
6*d*.	„ lilac.	

(Commercial seed.)

Type 7. Biennial " Brompton " stocks; leaves hoary; flowers white; seeds intermediate in colour, becoming much yellower on keeping.

7*a*.	Samples from various sources. 7*b* was represented by a single plant.
7*b*.	
7*c*.	

Type 8. Biennial " Brompton " stocks; leaves hoary; flowers reddish purple; seeds green.

8*a*.	Various plants of unknown origin which gave results not wholly uniform.
8*b*.	
8*c*.	

With the exception of 3*c*, 4, 7, and 8, which were not tested, all these varieties have been found to breed truly on self-fertilisation.

The colour of the seeds was found to be due to two distinct factors: to the colour of the embryo, and also to that of the testa—a structure belonging to the mother-plant—through which the embryo is seen. The testa though shading from lemon-yellow through bright-yellow to light-brown was always of this one class of colour, and as a rule of sufficient transparency to allow one to judge whether the colour of the underlying embryo was yellowish, or more or less deep green or green tinged with violet. It was therefore generally possible to classify the unskinned seeds; but in cases in which a more or less continuous series of tints was obtained it was not always easy to decide where to draw the dividing line, and in these instances sorting was not attempted. Consequently, the classification of seeds into brown and green is to be taken as indicating differences in the embryos. When seeds are described as of intermediate tint, it is not certain whether the embryo was greenish or truly intermediate, but in no such case would the embryo be the true yellow of the types. The only type which had a normally intermediate seed was 7.

In embarking on these experiments it was originally intended to investigate statistically the laws of inheritance operating in regard to hoariness and glabrousness. Experiment, however, soon revealed the fact that the results in regard to this specified character differed greatly according as one or other of the several varieties was used, and it became necessary to investigate also the properties of the other differentiating characters in their various combinations.

I. *First Cross-bred Generation.*

A. *Details as to Offspring of Hoary × Glabrous.* (*Table I.*)

From Table I it appears that when the hoary forms are employed as seed-parent, the hoary character is, except in one union (Experiment 10), completely dominant. Of about a 1000 individuals raised from such crosses between various hoary and glabrous strains, all were hoary. It is noticeable that when the form No. 2, which has only the underside of the leaves hoary ("half-hoary") was used, *the resulting plants were completely hoary like those bred from a completely hoary parent.* To this statement two individual offspring, which came of the half-hoary type, were the only exceptions out of more than 100 plants thus raised.

The exception to the rule of universal appearance of the hoary character is found in Experiment 10. In this experiment two sister plants belonging to the half-hoary type (2) when crossed with the glabrous form (5*a*) produced seventy-two plants all glabrous, although when crossed with another glabrous strain (6*c*) the same two individuals gave the usual result (Experiment 11). Now the sister plants were descended by two generations of self-fertilisation from a common grandparent, and both the glabrous strains with which they were crossed had also been raised by two successive self-fertilisations. Both the parent and the grandparent of the two half-hoary plants had, when crossed with the glabrous strains 5*b* and 6*a* respectively (see Experiments 7 and 1), produced the hoary form and the hoary form only, but whether the unusual result in the third generation is in any degree to be attributed to repeated self-fertilisation, the evidence to hand is not yet sufficient to determine. As against such a view, however, we have the result obtained in the experiment with the other glabrous form 6*c* (Experiment 11), in which no such effect was produced.

As regards seed-colour, green appears usually to be a dominant, brown a recessive character; but the intensity of the green colour may become so much diminished on crossing, that when seen through the brown testa, the net result may be a more or less intermediate tint.

As regards flower-colour the results were far more complex, the product of combinations of *identical* colours varying according to the particular strain employed. It will therefore be more convenient to treat the question of flower-colour when the results of the crosses glabrous × hoary detailed in Table II have also been considered.

B. *Details as to Offspring Glabrous × Hoary.*

From Table II it will be seen that in ten out of the fourteen fruits obtained in the first year (1897–8), from a cross between a *brown* seeded glabrous type and the *black* seeded hoary type 1 (Experiments

Table I.—Offspring obtained from the cross Hoary ♀ × Glabrous ♂.

Number of experiment.	Date.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.	Number of offspring.			Colour of corolla in offspring.†
						Hoary.	Inter.*	Glabrous.	
1	1897–98	2 × 6*a* ½ *H. wh. br.* × *G. lp. gr.*	2	3	Green	34	—	—	Medium purple.
2	..	2 × 5*c* ½ *H. wh. br.* × *G. r. br.*	2	3	Brown	16	—	—	Pink.
3	..	3*a* × 5*c* *H. wh. br.* × *G. r. br.*	2	2	Greenish	30	—	—	Medium purple.
4	..	3*b* × 5*c* *H. wh. br.* × *G. r. br.*	4	5	Brownish or greenish	48	—	—	Pink.
5	..	3*b* × 6*b* *H. wh. br.* × *G. dp. gr.*	2	2	Green	4	—	—	Medium purple.
6	..	3*b* × 6*c* *H. wh. br.* × *G. cl. gr.*	4	4	Green	21	—	—	Medium purple.
7	1898–99	(2 × self) × (5*b* × self) ½ *H. wh. br.* × *G. cr. br.*	1	1	Brown	47	1	—	Pink.
8	..	(2 × self) × (6*c* × self) ½ *H. wh. br.* × *G. cl. gr.*	1	1	Greenish	9	—	—	
9	..	(3*b* × self) × (5*b* × self) *H. wh. br.* × *G. cr. br.*	1	1	Brown	2	—	—	
10	1899–1900	[(2 × self) × self] ½ *H. wh. br.* × [(5*a* × self) × self] *G. wh. br.*	2	3	Brown	—	—	72	
11	..	× [(6*c* × self) × self] *G. cl. gr.*		3	Green and brownish	117	1	—	Bluish pink.

* Under the head "intermediate" are included all plants resembling type No. 2, or exhibiting any lesser degree of hoariness; since in such of the latter as were allowed to flower the calyx and ovary were always hoary, it is evident that these individuals are more correctly to be added to the hoary than to the glabrous columns in the statement of totals.

† When no colour is given for the corolla the plants were destroyed before flowering.

Number of experiment.	Date.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.	Number of offspring.			Colour of corolla in offspring.
						Hoary.	Inter.	Glabrous.	
12	1899–1900	[(3*b* × self) × self] × [(5*a* × self) × self] *H. wh. br.* × *G. wh. br.*	4	6	Green and few brown	194	—	—	Light purple.
13	..	[(3*b* × self) × self] × [(5*b* × self) × self] *H. wh. br.* × *G. cr. br.*	1	1	Inter.	3	—	—	Pink.
14	..	[(3*b* × self) × self] × [(6*c* × self) × self] *H. wh. br.* × *G. cl. gr.*	2	2	Green and greenish	13	—	—	Medium purple.
15	1900–01	1 × 5*b* *H. wh. bl.* × *G. cr. br.*	4	20	Green	371	—	—	
16	..	1 × 5*c* *H. wh. bl.* × *G. r. br.*	4	15	Green	119	—	—	
17	..	1 × 5*d* *H. wh. bl.* × *G. pk. wh. br.*	4	6	Green	77	—	—	
18	..	1 × 6*b* *H. wh. bl.* × *G. dp. gr.*	3	8	Green	145	—	—	

ABBREVIATIONS USED IN THE TABLES TO DENOTE LEAF-CHARACTER, FLOWER-COLOUR, AND SEED-COLOUR.

Leaves.—H, hoary; $\frac{1}{2}$H, half-hoary; G, glabrous.

Flowers.—cl., claret; cr., cream; li., lilac; bl. pk., bluish pink; p., purple; dp., dark purple; mp., medium purple; lp., light purple; rp., reddish purple; r., red; wh., white; pk. wh., pinkish white.

Seeds.—bl., black; br., brown; gr., green; in., intermediate.

Table II.—Offspring obtained from the cross Glabrous ♀ × Hoary ♂.

Number of experiment.	Date.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.		Colour of corolla in offspring.	
					Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
19	1897–98	5*a* × 1 *G. wh. br.* × *H. wh. bl.*	1	1	All	—	—	16	—	Dark purple	
20	,,	5*b* × 1 *G. cr. br.* × *H. wh. bl.*	1	2	All	—	—	23	—	,,	
			1	2	All	—	—	19	—	,,	
				1	30 (24 sown)			21	—	,,	
						17		—·	14		Cream.
							5	—	2		Cream.
*20	1900–01	,, ,,	1	6	All	—	—	63	—		
21	1897–98	5*c* × 1 *G. r. br* × *H. wh. bl.*	1	2	All	—	—	11	—	,,	
*21	1900–01	,, ,,	1	8	All	—	—	13	—		
22	1897–98	5*d* × 1 *G. pk. wh. br.* × *H. wh. bl.*	1	1	All	—	—	14	—	Medium purple	
				1	30			26	—	,,	
						1		—	1		Pinkish.
							6	—	6		Pinkish.
			1	1	48 (12 sown)			10	—	,,	
							3				
				1	37 (28 sown)			25	—	,,	
						4		2	—	Produced no flowers	
*22	1900–01	,, ,,	1	2	All	—	—	23	—		

Number of experiment.	Date.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.		Colour of corolla in offspring.	
					Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
23	1897-98	5*e* × 1 *G. bl. pk. br.* × *H. wh. bl.*	1	1	All ?	—	—	13	—	Medium purple	
				1	45 (26 sown)			23	—	”	
							6 (4 sown)	—	4		Bluish pink.
24	”	6*a* × 1 *G. lp. gr.* × *H. wh. bl.*	1	2	All (24 sown)	—	—	8	—	Light purple	
25	”	6*b* × 1 *G. dp. gr.* × *H. wh. bl.*	1	1	All (12 sown)	—	—	12	—	Dark purple	
*25	1900-01	” ”	1	4	All	—	—	20	—		
				5	All	—	—	71	18		
26	1897-98	6*c* × 1 *G. cl. gr.* × *H. wh. bl.*	1	1	All	—	—	21	6	Dark purple	Claret.
27	”	6*d* × 1 *G. li. gr.* × *H. wh. bl.*	1	1	All	—	—	22	—	Light purple	
28	”	6*c* × 3*a* *G. cl. gr.* × *H. wh. br.*	1	1	All	—	—	11	—	Pink	
29	”	6*d* × 3*a* *G. li. gr.* × *H. wh. br.*	1	1	All	—	—	14	—	Light purple	

19—23 without asterisks) the seeds were uniform in colour (green), and sample sowings yielded hoary plants only. In the four remaining fruits borne by some of the same individuals (Experiments 20 and 22) the seeds were mixed—green, intermediate (the embryos being either yellowish green, or green with yellow radicles), and brown—and gave rise to a mixed offspring. These green seeds, like those from fruits with green seeds *only*, gave rise to hoary plants, the brown seeds to glabrous plants, and the intermediates to both forms. In these experiments the hoary parent was *white* flowered. The glabrous parent was *either white*, *cream*, *red*, *or pinkish*. Nevertheless, irrespective of the colour introduced by the glabrous parent, all the *hoary* offspring were *purple* without exception. The glabrous offspring, however, invariably exhibited the colour of their glabrous parent.

When one individual belonging to each of the four *green* seeded glabrous strains was crossed with the same *black* seeded hoary type 1 (Experiments 24—27 without asterisks), the resulting seeds were of one type of colour, either pure or rusty green, and afforded no indication as to the nature of the future plants. A full sowing from one individual, and sample sowings from two others, produced forty-two plants all hoary; from the remaining individual a mixed offspring was obtained, in which as before the colour of the flowers of the glabrous plants resembled that of the glabrous parent. The hoary cross-breds were all purple-flowered.

Lastly from a cross (Experiments 28—29) between two of the same *green* seeded glabrous strains and a *brown* seeded hoary form, green seeds and hoary plants alone were obtained, although one of the glabrous parents was the identical individual which gave the mixed offspring when crossed with the hoary type No. 1. So far as this result can be regarded as conclusive (only twenty-five plants were raised), the dominance of the leaf-character and the seed-colour in this case appears to be complete.

The occurrence of a mixed (hoary and glabrous) offspring in the first cross-bred generation, as has been stated above, had been previously observed by Trevor Clarke in cases in which the glabrous form was used as the seed parent (see p. 13). The actual numbers, however, are not given by him, nor is it stated whether the mixture occurred in the case of every flower or even of every individual. As in our own experiments the mixed result was constant neither for all the individuals of one strain, nor for the different flowers on a single individual, it was proposed to repeat this experiment in the following year. Unfortunately no plants of the original hoary form type 1 survived the winters of 1898 and 1899, and as this species does not flower in its first season, it was impossible in these two years to repeat precisely the original crosses. Recourse was therefore had to such hoary Brompton stocks or other strains as were available at the moment. The glabrous parents were in each case descendants (by self-fertilisation) of the original plants.

In these unions of 1898–1900 (Table III), the occurrence among the offspring of a larger or smaller number of recessives (glabrous) was the rule rather than the exception. Complete prevalence of the hoary character was only obtained in the four experiments (30—33) in which the hoary parent was a purple-flowered Brompton stock, and in two out of the three cases in which the white-flowered Brompton form, 7*c*, was employed (Experiments 37 and 45). In the remaining cross with 7*c*, in all those with the other white-flowered Bromptons 7*a* and 7*b*, with the white-flowered annual 3*c*, and with the purple-flowered annual 4, the offspring included some recessives. Reference to the table, however, will show that in those cases in which the offspring were mixed, the mixed result was not given by every seed parent employed, but by particular individuals or even, indeed, by particular flowers. For in some cases in which several flowers on the same individual were crossed, the offspring of some were mixed and of others not. It is not surprising therefore that when the totals obtained in the different unions are compared, no constant proportion between the two characters is discoverable. So far, however, the irregularity of these results remains unexplained.

In regard to seed-colour, in the four experiments (42—45), where *green*-seeded glabrous strains were crossed with the white-flowered Bromptons (seeds intermediate) the results varied; twice the seeds were all green, once mixed, and once difficult to classify. When *brown*-seeded glabrous strains were crossed with the same white Bromptons (Experiments 35—41) the resulting seeds were never uniformly coloured, though occasionally all those in a single fruit were alike. Nevertheless, a comparison of the numbers failed to reveal any constant proportion between the various seed-colours. In the cases in which brown-seeded glabrous strains were crossed with purple-flowered forms (seeds green) we find the same irregular result as before in the cross with the annual type 4 (Experiment 34), but with the Brompton strains the case is very different (Experiments 30—32). In the unions with 8*b* and 8*c*, the green colour was completely dominant, with 8*a* equal numbers of brown and green seeds were produced, the colours being well-marked and without intermediates. This equality in the totals was further borne out by the figures obtained for each individual, but it is of interest to note that a similar uniformity of distribution did not always extend to the separate flowers. Although, as a matter of fact, every cross-bred fruit contained both seed forms, yet in some there were only one or two of one or other colour.

The occurrence here of both seed-colours recalls the mixed result obtained in some cases in the preceding year with the hoary type No. 1. In those cases, however, there was no constant proportion

Table III.—Offspring obtained from the cross Glabrous ♀ × Hoary ♂.

In these experiments the seed-parent was the result of one or two self-fertilisations.

No. of expt.	Date. 1898—99, 1899—1900	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.*		Colour of flower in offspring.	
					Green.	Interm.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
30	..	(5*b* × self) × 8*a* *G. cr. br.* × *H. rp. gr.*	8	4	105		101	98 83	— —	Purple Red	
				2	46		57	45 46	— --		
				4	99		89				
				2	51		59				
				2	21		20				
				4	49		55				
				2	40		37				
				1	4		8				
		Total....	8	21	425	—	426	272	—		
31	..	[(5*b* × self) × self] × 8*b* *G. cr. br.* × *H. rp. gr.*	4	4	All	—	—	26	—	Purple	
32	..	[(5*a* × self) × self] × 8*c* *G. wh. br.* × *H. rp. gr.*	2	2	All	—	—	27	—	Purple	
33	..	[(6*c* × self) × self] × 8*b* *G. cl. gr.* × *H. rp. gr.*	2	2	All	—	—	39	--		
34	..	[(5*a* × self) × self] × 4 *G. wh. br.* × *H. p. gr.*	1	1	1	14	24	15	22	Purple	White
35	..	(5*b* × self) × 7*a* *G. cr. br.* × *H, wh. in.*	8	19	221	71	331	332	—		

			1 3	3 1 12	8 — 65	75 — —	— 35 484	46 34 260	— 1 16	Red	Cream
		Total....	12	35	294	146	850	672	17		
36	..	(5*b* × self) × 7*b* *G. cr. br* × *H. wh. in.*	1	1	3	17	11	13	8		Cream
37	..	[(5*b* × self) × self] × 7*c* *G. cr. br.* × *H. wh. in.*	2	5	93	71	65	155	—	Pink	
38	..	(5*a* × self) × 7*a* *G. wh. br.* × *H. wh. in.*	1	3	95	—	7	92	7	Purple	
39	..	(5*a* × self) × 7*b* *G. wh. br.* × *H. wh. in.*	7	18	483	34	63	440	27	Purple	
40	..	[(5*a* × self) × self] × 7*c* *G. wh. br.* × *H. wh. in.*	2	2	2	49	8	50	7		
41	..	(5*d* × self) × 7*a* *G. pk. wh. br.* × *H. wh. in*	3	8	—	26	235	236	11	Pink	Pinkish white
42	..	(6*c* × self) × 7*a* *G. cl. gr.* × *H. wh. in.*	6	21	All	—	—	382	44	Purple	—
43	..	(6*c* × self) × 7*b* *G. cl. gr.* × *H. wh. in.*	3	12	∝		 39	339 —	17 38	Purple	 Claret
		Total....	3	12	∞	—	39	339	55		
44	..	(6*b* × self) × 7*b* *G. dp. gr.* × *H. wh. in.*	1	1	All	—	—	31	8		
45	..	[(6*c* × self) × self] × 7*c* *G. cl. gr.* × *H. wh. in.*	3	3	Not classified			71	—		
46	..	[(5*b* × self) × self] × 3*c* *G. cr. br.* × *H. wh.* ?	2	2	96	2	4	33	4	Purple	Cream
47	..	[(5*a* × self) × self] × 3*c* *G. wh. br.* × *H. wh.* ?	2	2	59	—	4	57	2	Purple	White
48	..	[(6*c* × self) × self] × 3*c* *G. c'. gr.* × *H. wh.* ?	1	1	All	—	—	6	5	Purple	Claret

Generally speaking, when the seeds were mixed and gave rise to mixed plants, the glabrous plants arose from brown seeds.

* In this and all succeeding tables a blank space opposite the seed numbers indicates that these seeds were not sown.

between the two colours, and, on the other hand, brown seed-colour was correlated with glabrous leaf-character. It should, however, be stated that the seed-*colour* purity of the type 8*a* was not separately tested, as was done in the case of type 1, and that the production of *equal* numbers of the two seed-colours is precisely the result which we should expect if 8*a* were not a pure colour form, but itself a cross-bred in this respect. This possibility cannot now be disproved; but it may be noted that Trevor Clarke obtained a like result from a cross between a brown-seeded and a black-seeded form, 50 per cent. of the seeds coming black.

Finally in the remaining union (Experiment 33), in which both parents were green seeded, the resulting seeds were all green.

A further attempt to obtain confirmation of these results was made, especially in view of the appearance at this point of Correns'* "Levkojenbastarde." Commenting upon Trevor Clarke's results, which are at variance with his own observations regarding the complete dominance of the hoary character, he suggests that the occurrence of a mixed offspring in the first generation is to be attributed to subsequent (? self) fertilisation. Such an explanation, however, takes no account of the alteration in habit of the glabrous plants which Trevor Clarke describes, a fact which would seem to vindicate the accuracy of his experiments.† It seems equally unlikely that the exceptions to the universal appearance of the hoary character observed in our own experiments are to be attributed to experimental error; for it is difficult to believe that in cross-fertilisations with, *e.g.*, white-flowered and purple-flowered Brompton strains, carried out at the same time, and sometimes upon the same individuals, an error should frequently occur in the former unions and never in the latter. As, however, some more plants of the hoary type No. 1 had in the meantime been successfully raised, an exact repetition of the original experiment was now performed with the added precaution that in the case of the glabrous parents all unemasculated flower-buds were removed before the dehiscence of the anthers. (Experiments marked with *, Table II.) In this way any possibility of error arising from the presence of thrips or other insect too minute to be excluded by the muslin cover, which might carry pollen from one flower to another, was avoided.

Once again a confirmation of the earlier results was obtained, for in one of the unions (6*b* × 1, Experiment 25*), in which several flowers on one individual had been crossed, some of the cross-bred fruits yielded a mixed offspring, while from others hoary plants only were obtained.

From the sum of these results it is evident that in the cross glabrous × hoary, the hoary character appears in the offspring in the vast majority

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* 'Bot. Cblt.,' 1900, vol. 84.

† Unfortunately, in the similar cases herein described, no reliable observations on this question of habit were recorded.

of cases; but further experiments are needed in order to determine how far we are here dealing with a question of strain, of the individual, or even of separate flowers, or to what extent, if any, these results are dependent upon varying conditions.

Subsequent experiments, which will be set forth in detail hereafter, showed that the constitution of the dominant offspring, produced in these crosses, differed radically from that of the recessives. For while the former (hoary) were proved to give rise to mixed offspring in fair accordance with Mendelian expectation, the latter (glabrous) *behaved as pure glabrous forms, giving rise to glabrous offspring only, when self-fertilised.*

This phenomenon is discussed hereafter in connection with others of a like nature (p. 154).

C. *Flower-colour of First Cross-bred Generation.*

To return to the question of flower-colour, the results in both sets of experiments (A and B) may be most easily gathered from the following schedule, in which the various unions giving an identical result are grouped together in each column.

In regard to the recessive offspring such a schedule is unnecessary, since in each case the flower-colour of recessive offspring resembles that of the recessive parent, though whether the shade was identical in all cases is not certain.

In the table (p. 46), the crosses hoary × glabrous and glabrous × hoary have been separated for convenience of reference, but there is no reason to suppose any significance (in regard to flower-colour) to attach to the circumstance of the way the cross was made. Flower-colour was not a primary subject of these experiments, and, as it happens, no true reciprocals were flowered.

The coloured forms red, pink, purple, claret, have not yet been crossed *inter se.*

In each case one parent was white, except in one instance when cream was crossed with purple (13). *No white* offspring were produced in first crosses. In some cases there was obvious blending, as for example when white crossed with red or claret, gave pink. More often the result was a wholly new colour, and except in four cases (6, 9, 27, 13*b*), always some shade of purple, but varying in tint even in crossings of similar colours according to the particular strains employed. Not only are such purple offspring produced when some of the coloured forms are crossed with white, but even in the crosses *between two distinct white forms* (10, 19, 24). Possibly we have here a reappearance of the colour commonly occurring in the wild species (*incana*), from which the hoary garden stocks may have originated—a case in fact of "reversion" (see p. 144). In the four exceptions 6, 9, 27, 13*b*, in which cream was

Colours of Flower in DOMINANT *Cross-breds.*

Form of union : Hoary × Glabrous.

Dark purple.	Medium purple.	Pale purple.	Pink.	Red.
	(1) white 2 × pale purple 6*a* (2) white 3*a* × red 5*c* (3) white 3*b* × medium purple 6*b* (4) ,, × claret 6*c*		(5) white 2 × red 5*c* (6) ,, × cream 5*b* (7) ,, × claret 6*c* (8) white 3*b* × red 5*c* (9) ,, × cream 5*b*	
		Form of union : Glabrous × Hoary.		
(10) white 5*a* × white 1 (11) red 5*c* × ,, (12) cream 5*b* × ,, (13*a*) ,, × purple 8*a* (14) medium purple 6*b* × white 1 (15) claret 6*c* × ,, (16) ,, × white 7*a*	(17) pinkish white 5*d* × white 1 (18) bluish pink 5*e* × ,, (19) white 5*a* × white 7*a* (20) claret 6*c* × white 7*b*	(21) pale purple 6*a* × white 1 (22) lilac 6*d* × ,, (23) ,, × white 3*a* (24) white 5*a* × white 7*b*.	(25) pinkish white 5*d* × white 7*a* (26) claret 6*c* × white 3*a*	(27) cream 5*b* × white 7*a* (13*b*) ,, × purple 8*a*

crossed with white or purple, we have the unexpected appearance of pink or red; a similar occurrence was observed by Correns among the offspring of cross-breds whose parents had "yellowish white" and "violet" flowers respectively.

In connection with the question of colour one point of interest may be briefly mentioned here, viz., the occurrence of "flaking." Although this phenomenon was occasionally observed in the coloured pure strains, even when repeatedly self-fertilised, it was not very common; among the coloured cross-breds, however, it was almost universal. Plants which at first produced exclusively self-coloured flowers, as the season advanced bore flowers speckled or streaked with white. In some cases the last flowers were even entirely white. Such flaking was recorded in thirty-one out of thirty-nine combinations in the first year, and in forty-one out of forty-three in the second.*

D. *Seed-colour of First Cross-bred Generation.*

When brown-seeded and green-seeded types (including "black") were intercrossed, green was generally dominant, though exceptions were seen. When browns were crossed with the intermediate type 7, the results were irregular. Similarly when greens were crossed with these intermediates the results were sometimes irregular. When browns were crossed with browns, the one being glabrous and the other hoary, the result was four times brown, once greenish, once intermediate, and twice a mixture. Green (including "black") with green always gave green.

When in first crosses *glabrous* plants were produced, these arose from seeds similar to those of the glabrous parent, except in one case where the intermediate type 7 was used. In that case glabrous plants came from both *green* and *brown* seeds.

II. *Posterity of Cross-breds.*

The offspring of cross-breds will be described in the following order:—

1. Offspring of cross-breds produced from (D × R).†

   A. *When D and R were brown-seeded and green-seeded respectively.*

   a. When the cross-breds were fertilised with a recessive form. (Table IV.)
   b. When the cross-breds were self-fertilised. (Table V.)
   c. Subsequent posterity derived from the foregoing. (Table VI.)

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* Such flaking is exceedingly common in the *late* flowers of Sweet Peas.

† In what follows, the classification into D, dominant, and R, recessive, refers to the characters hoariness and glabrousness, respectively.

B. *When D and R were both brown-seeded.*

a. When the cross-breds were fertilised with a recessive form. (Table VII.)
b. When the cross-breds were self-fertilised. (Table VIII.)
c. Subsequent posterity derived from the foregoing. (Table IX.)

It was thought desirable to present the set of results contained in A separately from those in B, since the wholly unexpected results obtained in B (section *a*) were absent from the corresponding section in A.

2. Offspring of cross-breds produced from (R × D).

a. When the cross-breds were fertilised with a recessive form. (Table X.)
b. When the cross-breds were self-fertilised. (Table XI.)
c. Offspring of dominant cross-breds produced in 2*a*. (Table XII and Table XIII.)
d. When the cross-breds were fertilised with a dominant form.

Under these heads we have to consider the results of self-fertilising cross-breds (DR × self) and also the results of fertilising cross-breds with recessive (DR × R) and dominant (DR × D) forms. Subsequently we shall have to describe in each case experiments in which offspring so produced were fertilised again with recessives, and so on. To denote the recessive parentage the expressions R_1, R_2, R_3 are employed. In any one expression the numbers denote the order in which distinct recessive strains were introduced into the pedigree.

1. A. *Offspring of Cross-breds (D × R) when D and R were brown-seeded and green-seeded respectively.*

a. *When the Cross-breds were Fertilised with a Recessive Form.*

From Table IV it will be seen that when the cross-breds (2 × 6*a*) were crossed with the recessive form (6*c*) (produced by self-fertilisation), the resulting fruits always contained a mixture of seeds—usually green and dark brown (only in three seeds was the true light-brown of the original parent (type 2) observed); in twenty-two other seeds the colour was difficult to classify. Excluding these last, the total numbers for the two colours are roughly equal, nor is the departure from this result in the case of individuals ever considerable. Each kind of seed gave rise to both forms of plants, and in about equal numbers, the slight deviations in the totals being complementary. In brief, as regards both seed-colour and leaf-surface, we find the Mendelian ratio 1 : 1. The flowers were either bluish-pink or purple, except in two glabrous plants in which they were white becoming tinged later; there appeared to be a well marked though not an absolute correlation between seed- and flower-colour. With few exceptions the pinkish flowers were derived from the brown seeds, and the purple from the green, so that as regards flower-colour the recessive offspring derived from brown seeds more nearly resembled their recessive parent, those from green seeds their more remote recessive progenitor.

In the parallel experiment with (3*b*), the seeds were uniformly coloured (green) but every individual produced a mixed offspring, though the final result (Experiment 50) was rather farther from the ratio 1 : 1.

b. *When the Cross-breds were Self-fertilised.*

The results recorded in Table V were obtained when the identical cross-breds employed as seed parents in Experiment 49 were self-fertilised instead of being crossed with a recessive form. The seeds, more difficult to sort than in the previous case, again showed a rough equality in the two type-colours, but the percentage of intermediates was much greater than before. From each individual and from each kind of seed a mixture of plants was obtained, the green and intermediate seeds giving rise to a majority of hoary, the brown to a majority of glabrous plants. The totals, however, showed a proportion of glabrous plants *far in excess* of the theoretical ratio of 1 : 3.

The above results will be considered in connection with those obtained in the next generation.

Table IV.—Offspring obtained from Fertilising the Cross-breds (D × R) with a Recessive Form, when D and R were brown-seeded and green-seeded respectively.

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Glabrous.
49	(2 × 6*a*) × (6*c* × self) (½*H.wh.br.* × *G.lp.gr.*) × *G.cl.gr.*	1	2	24			*gr.* 12	—	*gr.* 11	Purple (various)	Purple (various) and pinkish.
						35	*br.* 16	—	*br.* 8	Pinkish except 1 purple	Pinkish except 1 purple.
			1	26			*gr.* 10	—	*gr.* 13	Purple (various)	Purple (various).
					3		*in.* —	—	*in.* 3		
						19	*br.* 12	—	*br.* 7	Pinkish	Pinkish.
		1	2	31			*gr.* 5	—	*gr.* 15	Purple (various)	Purple (various) and pinkish.
						37	*br.* 18	—	*br.* 16	Pinkish	Pinkish.
			2	37			*gr.* 15	—	*gr.* 13		
						39	*br.* 17	*br.* 1	*br.* 13		
		1	2	36			*gr.* 16	—	*gr.* 17	Purple (various)	Purple (various).
						54	*br.* 21	—	*br.* 22	Pinkish	Pinkish.
			1	30			*gr.* 11	—	*gr.* 12		
						24	*br.* 10	—	*br.* 13		
		1	2	38			*gr.* 14	—	*gr.* 15	Purple (various) and pinkish	Purple (various) and pinkish.
						18	*br.* 6	—	*br.* 11	Pinkish	
			2	7			*gr.* 5	—	*gr.* 2	Purple (various)	Purple.
					19		*in.* 8	—	*in.* 7		
						6	*br.* 3	—	*br.* 3		

			3	66			*gr.* 31	—	*gr.* 31	Purple (various)	Purple (various).
		1				62	*br.* 40	*br.* 2	*br.* 23	—	Purplish-white.
			2	54			*gr.* 27	—	*gr.* 22	Purple (various)	Purple (various) except 1 white.
						41	*br.* 20	—	*br.* 19	Pink (various)	Pink (various).
		1	1	15			*gr.* 4	—	*gr.* 9		
						15	*br.* 7	—	*br.* 8		
			1	26			*gr.* 12	—	*gr.* 14		
		1				21	*br.* 9	—	*br.* 11		
			1	16			*gr.* 8	—	*gr.* 7		
						14	*br.* 6	—	*br.* 7		
			2	56			*gr.* 25	—	*gr.* 31	Purple (various)	Purple (various).
		1				47	*br.* 20	—	*br.* 26	Pinkish	Pinkish.
			2	25			*gr.* 11	—	*gr.* 13	Purple (various)	Purple (various).
						30	*br.* 11	—	*br.* 15	1 pinkish	1 white.
	Total…………	8	26	487	22	462	430	3	437		
	(3*b* × 6*b*) × (6*c* × self)	1	1	All	—	—	21	—	16		
		1	1	”	—	—	20	—	12		
50	(*H.wh.br.* × *G.dp.gr.*) × *G.cl.gr.*	1	1	”	—	—	18	—	14		
		1	2	”	—	—	50	—	30		
			3	”	—	—	39	—	47		
		1	1	”	—	—	14	—	19		
		1	1	”	—	—	38	—	42		
		1	1	”	—	—	18	—	17		
		1	4	”	—	—	90	—	61	Purple (various)	Purple (various).
		1	1	”	—	—	18	—	24		
		1	1	”	—	—	8	—	13		
	Total…………	10	17	All	—	—	334	—	295		

Table V.—Offspring obtained from the Self-fertilisation of the Cross-breds (D × R), when D and R were brown-seeded and green-seeded respectively.

No. of expt	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.		
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Inter.	Glabrous.
51	(2 × 6*a*) × self (½*H. wh. br.* × *G. lp. gr.*)	1	3	36	51	30	*gr.* 22 *in.* 32 *br.* 9	— *in.* 1 *br.* 5	*gr.* 13 *in.* 15 *br.* 16	Purple and Purplish-white. Purple and Purplish-white. As the cross-bred and its recessive parent were both purple, there is no clear indication how the flower-colour descended. Absence of pure whites should be noted.		
		1	4	56	62	55	*gr.* 25 *in.* 30 *br.* 10	— — *br.* 6	*gr.* 8 *in.* 15 *br.* 13			
		1	3	58	38	41	*gr.* 39 *in.* 24 *br.* 6	— *in.* 1 —	*gr.* 5 *in.* 11 *br.* 32			
		1	6	71	58	58	*gr.* 34 *in.* 39 *br.* 6	— *in.* 2 —	*gr.* 20 *in.* 10 *br.* 24			
		1	4	62	58	36	*gr.* 40 *in.* 39 *br.* 1	— — —	*gr.* 13 *in.* 17 *br.* 13			
		1	3	60	11	52	*gr.* 35 *in.* 7 *br.* 15	— — *br.* 3	*gr.* 10 *in.* 3 *br.* 20			

No. of expt.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.		
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Inter.	Glabrous.
		1	4	58	30	46	*gr.* 30 *in.* 15 *br.* 11	— — —	*gr.* 10 *in.* 11 *br.* 24			
		1	3	48	41	38	*gr.* 21 *in.* 23 *br.* 5	— — —	*gr.* 22 *in.* 13 *br.* 32			
		1	2	21	—	47	*gr.* 12 — *br.* 14	— — —	*gr.* 4 — *br.* 17			
		1	?	225	112	241	*gr.* 121 *in.* 76 *br.* 60	— — *br.* 22	*gr.* 39 *in.* 16 *br.* 87			
		10	32 + ?	695	461	644	801	40	533			

c. *Subsequent Posterity derived from the foregoing* (*Table VI*).

In Experiments 52 and 53 (Table VI) we have results similar to those given in Table IV, the ratio of D to R being again not far from 1 : 1.

In Experiment 54, as in the comparable case in the preceding generation (Table V), we find that the number of glabrous plants is far too high; but that when the more hoary form *3b* is substituted for the less hoary form 2 (Experiment 55), the result is exact—3D : 1R.

In Experiment 56, in which we should expect either 3D : 1R or else only dominants, according as the individual happened to be a DR or a pure D, it appears that three of the five individuals selected at random were DR and the remaining two pure D. Some of the offspring of the two latter plants, however, and also of one of the former, were half-hoary like the original hoary parent (type 2), or were even less hoary still, so that when quite young they might easily be mistaken for glabrous plants. Among the offspring of all the DR individuals there was the usual high percentage of recessives. In Experiment 57, a plant approaching the half-hoary character of type 2 (raised from (2 × 6) × self in Experiment 51) gave on self-fertilisation no offspring fully hoary, but only intermediate and glabrous plants.

Lastly, in the five remaining trials (Experiment 58), in which the seed parents were of recessive form, we have the expected proof of the purity of such recessives; for whether self-fertilised or crossed with a pure recessive, they invariably yielded recessives only.

To sum up the results in the two generations, we may conclude that Mendel's law holds for all the above cases except those in which a hoary cross-bred *originally derived from the half-hoary form* (2) is self-fertilised. In such cases the glabrous offspring are constantly in excess of the theoretical proportion of 1 : 3, while the hoary offspring often include many plants which exhibit various intermediate degrees of hoariness.

B. *Offspring of Cross-breds* (*D* × *R*) *when D and R were both brown-seeded.*

a. *When the Cross-breds were Fertilised with a Recessive Form.*

The results of the various experiments recorded in Table VII are strikingly different among themselves and altogether unexpected.

In Experiment 59, although the three pure forms 2, 5*c*, 5*a*, and the cross-bred parent (2 × 5*c*) were all brown seeded, yet the fruits resulting from the cross (2 × 5*c*) × 5*a* contained seeds of at least *two* colours—brown and green.

The colours were well-marked, less than 1 per cent. being classed as intermediates. With two or three exceptions the numbers in individual fruits (and naturally therefore in individual plants) showed a rough equality.

Table VI.—Experiments 52—58.

Number of experiment.	Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.			Expected result.
				Hoary.	Inter.	Glabrous.	
	[(D × R_1) × R_2] × R_2. Seed parent hoary.						
52	[(2 × 6*a*) × (6*c* × self)] × [(6*c* × self) × self]	7	12	262	—	231	1D : 1R.
53	[(3*b* × 6*b*) × (6*c* × self)] × [(6*c* × self) × self]	2	3	36	—	42	,,
	[(D × R_1) × R_2] × self. Seed parent hoary.						
54	[(2 × 6*a*) × (6*c* × self)] × self	7	34	312	8	162	3D : 1R.
55	[(3*b* × 6*b*) × (6*c* × self)] × self	2	8	82	—	28	,,
	[(D × R_1) × self] × self. Seed parent hoary.						
56*a*	[(2 × 6*a*) × self] × self	3	3	33	—	14	3D : 1R, or all D, according as [(D × R_1) × self] was DR or D.
			5	68	—	29	
			4	90	7	53	
56*b*		2	4	88	32	—	
			6	—	78	—	
	[(D × R_1) × self] × self. Seed parent intermediate.						
57	[(2 × 6*a*) × self] × self	2	5	—	17	58	No definite prediction as to the result of this fertilisation was possible, since the plant used was neither half hoary like the one original parent, nor glabrous like the other, but intermediate between the two.
	[(D × R_1) × R_2] × R_2. Seed parent glabrous.						
58*a*	[(2 × 6*a*) × (6*c* × self)] × [(6*c* × self) × self]	11	?	—	—	583	All R.
58*b*	[(3*b* × 6*b*) × (6*c* × self)] × [(6*c* × self) × self]	2	2	—	—	56	,,
	[(D × R_1) × R_2] × self. Seed parent glabrous.						
58*c*	[(2 × 6*a*) × (6*c* × self)] × self	11	44	—	—	537	,,
58*d*	[(3*b* × 5*c*) × (5*a* × self)] × self	2	6	—	—	9	,,
	[(D × R_1) × self] × self. Seed parent glabrous.						
58*e*	[(2 × 6*a*) × self] × self	3	8	—	—	56	,,

Table VII.—Offspring obtained from Fertilising the Crossbreds (D × R) with a Recessive Form, when D and R were both brown-seeded.

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.		
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Inter.	Glabrous.
59	(2 × 5*c*) × (5*a* × self) (½ *H.wh.br.* × *G.r.br.*) × *G.wh.br.*	1	1	13		9						
			1	21		17						
			1	5		8						
		1	2	30		35						
			1	7	6	22						
		1	2	33		44						
		1	1	17		16						
			1	11		16						
			1	15	2	15						
		1	2	42		50						
			1	24			23	—	—	Purple.		
						19	—	—	19			White.

			3	42			41	—	—			
						42	—		41			
			2	40			39	—	—			
		1				44	—	—	42			
			1	9								
						10						
			1	16			16	—	—	Purple.		
						34	—	—	30			White.
			1	15								
						15						
		1	1	18								
						18						
			1	19								
						23						
		1	2	29								
						34						
	Total.........	8	26	406	8	471	119	—	132			
60	(2 × 5*c*) × (5*b* × self) (½*H.wh.br.* × *G.r.br.*) × *G.cr.br.*	1	4	not classified			121	—	2			
		1	2	,,	,,		33	1	2	Red and bluish-pink	White	Pinkish.
		1	5	,,	,,		94	3	11			
	Total.........	3	11				248	4	15			
61	(3*a* × 5*c*) × (5*a* × self) (*H.wh.br.* × *G.r.br.*) × *G.cr.br.*	1	1	41	—	—						
		1	1	30	—	—	25	—	—			
		1	1	40	—	—	35	—	—			
			5	133 (20 sown)	—	—	17	—	—	Purple.		
					2		2	—	—			
						2	—	—	1			Red.
	Total.........	3	8	244	2	2	79	—	1			

Table VII—*continued.*

No. of expt.	rentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.		
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Inter.	Glabrous.
62	$(3a \times 5c) \times (5b \times \text{self})$ $(H.wh.br. \times G.r.br.) \times G.cr.br.$	1	3	30			28	—	—	Purple (various).		
					2		2	—	—			
						53	52	—	—	Red, except 1 pink.		
		1	2	23			22	—	—			
						46	40	—	—			
		1	1	16 (10 sown)			10	—	—	Purple.		
						18 (10 sown)	9	—	—	Red, pink, and bluish-pink.		
	Total	3	6	69	2	117	163	—	—			
63	$(3b \times 5c) \times (5a \times \text{self})$ $(H.wh.br. \times G.r.br.) \times G.wh.br.$	1	1	27	—	—	23	—	—	Purple.		
		1	1	7 (5 sown)			5	—	—	Purple.		
						13 (5 sown)	3	—	2	Red, pink, and white		White.
			1	27			27	—	—			
						1	1	—	—			
		1	1	11			11	—	—			
					43		25	—	—			
						8	4	—	3			

		1	2	53	—	—	51	—	—			
		1	1	34			5	—	—			
					5		3	—	2			
						3	1	—	2			
	Total........	5	7	159	48	25	159	—	9			
64	(3*b* × 5*c*) × (5*b* × self) (*H.wh br.* × *G.r.br.*) × *G.cr.br.*	1	1	—	—	4	3	—	—	Red and pink.		
65	(2 × 5*c*) × (6*c* × self)	1	1	21			13	—	7			
	($\frac{1}{2}$*H.wh.br.* × *G.r.br.*) × *G.cl.gr.*					18	4	—	13			
		1	1	15			8	—	7			
						18	9	—	9			
	Total....	2	2	36	—	36	34	—	36			

Sample sowings* (in each case of more than 100 seeds) further showed that the green seeds gave rise to hoary plants bearing purple flowers, a colour not found in either parents or grandparents, and the brown seeds to glabrous plants with white flowers like those of their recessive parent, and dominant grandparent. We may therefore conclude that the rough equality in the totals for seed-colour indicates in this case a corresponding agreement in the totals for the two kinds of plants differentiated as to flower-colour, and fair consistency with Mendel's ratio. There are indications that such correlation between the flower-colour and the leaf-character may sometimes, as here, be definite, though the experiments show considerable irregularities in this respect. (The 8 intermediates were not sown.)

In Experiment 60 in which (5*b*) was employed in place of (5*a*), the seeds though varying from brown to greenish were mostly of a nondescript intermediate tint difficult to classify. As the seeds could not be satisfactorily sorted all were sown, *and* 252 *hoary* (*including* 5 *intermediates*) *and only* 15 *glabrous plants* were obtained instead of 3 : 1. The latter plants bore pink flowers. Of the former some fifteen specimens were grown to maturity, and bore flowers varying from red to bluish-pink. Coincident with the absence of typical green seeds, we have the complete disappearance of the purple flowers characteristic of the corresponding offspring in the preceding experiment, and the occurrence of the red or pink shades frequently observed after a cross with 5*c* (red) or with the cream-coloured form 5*b*. The intermediates bore white flowers like their intermediate grandparent.

Results somewhat similar as regards the character of the offspring, and equally at variance with the expected ratio, were obtained from two other unions (Experiments 61 and 63). In both these cases only a very small proportion of the offspring were glabrous (79D 1R and 159D 9R). Of these the one in Experiment 61 resembled its more remote recessive progenitor R_1 in flower-colour (red); the two which flowered in Experiment 63 were white like their recessive parent R_2, and also their dominant grandparent.

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* When the seeds were sorted, those obviously bad were discarded; the numbers given in the tables therefore only include such as appeared likely to germinate.

When the seeds were of mixed colours, a sample sowing of those which presented some definite colour sometimes sufficed to indicate the character (whether hoary or glabrous) of the whole class. If a uniform result was obtained the remainder of the same class were not sown.

But in regard to other seed-colour categories, want of uniformity of tint, or the occurrence of a mixed result as regards leaf character, made a full sowing necessary. In such cases the calculated totals of hoary and glabrous plants are based upon the *total* numbers of each seed-colour irrespective of the *particular* number of any colour which failed to germinate. The assumption that equal proportions of the differently coloured seeds would have failed to germinate may, however, introduce an appreciable error.

In Experiment 64 the offspring were too few (three) to give a decisive result.

In Experiment 62 the disappearance of the recessive form appears to be complete; *for we have the remarkable result that out of a total offspring numbering* 163, *not a single plant was glabrous*, though two of these seed-plants gave mixed offspring on self-fertilisation in Experiment 67. Finally, in Experiment 65, in which R_2 differs in seed-colour from R_1, we have a Mendelian result, both as regards seed-colour and leaf-character. These results will be considered in connection with the general statement of conclusions.

In regard to seed-colour the results were no less puzzling. In all cases the seeds were mixed. In the two experiments (59 and 65) in which a nearly Mendelian result was obtained, we find complete correlation between seed-colour and leaf-character in the former, and distinct evidence to the contrary in the latter. In Experiment 63 the correlation is imperfect; green seeds produced hoary plants, but brown seeds produced both forms. In Experiment 61 there is also some indication of correlation. In Experiment 62, on the other hand, the seed-colours afforded no clue, for all alike gave rise to hoary plants.

These results will be discussed hereafter. Attention must be directed to the fact that while on the one hand unions in the form $DR_1 \times R_2$ gave Mendelian results in both trials in which R_1 and R_2 were green-seeded, and in the one trial in which R_1 was brown-seeded and R_2 green-seeded; those in which R_1 and R_2 were both brown-seeded did so in one case only out of five. It is characteristic of these aberrant cases that there is an overwhelming preponderance of dominants. This discrepancy is certainly not fortuitous; *for either the one or the other result can be obtained from the same DR individual by an appropriate selection of the second recessive parent.* (See Experiments 85 and 87.)

What determines the several results is entirely unknown. R_1 differs from R_2, so far as we can tell, in nothing but colour.

b. When the Cross-breds were Self-fertilised.

Turning now to the results obtained on self-fertilisation (Table VIII), in Experiment 66, as in the previous case in which the half-hoary form (2) was used (Experiment 51), the glabrous offspring were far in excess of the Mendelian proportions of 1 : 3. Allowing for the possibility that seedlings which "damped off" very early, classified as glabrous, may, in reality, have been intermediates, the excess would remain considerable. The flowers of the glabrous offspring were white or pink, not red as in the recessive parent; those of the hoary plants white, pink, or red. The seeds were not classified.

In Experiment 67 there is a similar discrepancy between the expected and the observed results, 245D 131R instead of 3 : 1, although in this case the dominant parent (3*a*) was a fully hoary

Table VIII.—Offspring obtained from the Self-fertilisation of the Cross-breds (D × R) when D and R were both brown-seeded.

No. of expt.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Glabrous.
66	(2 × 5*c*) × self	1	4	Not classified			62	12	35	Red, white, and bluish-pink	Pink, white, and pinkish-white.
		1	6	,, ,,			61	5	42		
	(½ *H. wh. br.* × *G. r. br.*)	1	2	,, ,,			42	2	22		
		1	5	,, ,,			50	6	40		
		1	3	,, ,,			63	5	35		
		1	1	,, ,,			14	5	1		
		1	3	,, ,,			80	16	44		
		1	1	,, ,,			16	1	19		
	Total	8	25				388	52	238		
67	(3*a* × 5*c*) × self	1	1	6			5	—	1	Purple (various) Pink, white, and bluish-pink	Purple (various). Pink.
						24	15	—	9		
	(*H. wh. br.* × *G. r. br.*)	1	1	10			8	—	2		
						25	17	—	8		
		1	?	110			51	—	34		
					121		53	—	30		
						15	7	—	7		
		1	?	63			43	—	15		
					63		42	—	20		
						11	4	—	5		
	Total ...	4	2 + ?	189	184	75	245	—	131		

No. of expt.	Parentage.	Number of seed parents.	Number of flowers.	Colour of resulting seeds.			Number of offspring.			Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Inter.	Glabrous.	Hoary.	Glabrous.
68	(3*b* × 5*c*) × self	1	2	—	—	All	49	—	11		
	(*H. wh. br.* × *G. r. br.*)	1	1	—	—	,,	30	—	9		
		1	1	—	—	,,	21	—	8		
		1	?	—	—	,,	31	—	9		
		1	?	—	—	,,	221	—	81		
	Total	5	4 + ?	—	—	All	352	—	118		

form. The flowers of plants, whether glabrous or hoary, derived from green seeds, were purple; those from brown seeds, pink or more rarely white; on the other hand, there appeared to be *no* correlation between *seed-colour* and *leaf-character* in this particular case.

In Experiment 68 we have the exact result 3D : 1R. The seeds, unlike those in the two preceding experiments, were all of one colour, brown. The plants were destroyed before flowering.

The results in Experiments 66 and 68 confirmed those obtained in Experiments 51, 54, 55. The cross-breds *3b* × a recessive (whether green- or brown-seeded) gave a Mendelian result on self-fertilisation; whereas hybrids arising from the half-hoary type 2 × a recessive gave, on self-fertilisation, more than half the total offspring recessive. In Experiment 67—the case of cross-breds *3a* × *5c*—though *3a* is a form to all appearances similar to *3b*, the result of self-fertilisation is of the same exceptional character as that given by the cross-breds containing the half-hoary type.

c. Subsequent Posterity derived from the foregoing.

In Experiments 69—74 we have results obtained from a third crossing with a recessive form, when R_2 was again used as the recessive parent $(DR_1 \times R_2) \times R_2$. All the individual matings in four combinations, and seven out of eight matings in the fifth combination (Experiment 73), gave results in good agreement with the expected 1D : 1R. The exceptional individual in the fifth combination gave all (twenty-one) dominants. This individual had red flowers, whereas the other seven plants were various shades of purple. In the remaining combination, however (Experiment 72), the numbers obtained showed a ratio of 2D : 1R; nor could the total result be traced (as in Experiment 73) to the exceptional behaviour of individuals. From each fruit, as well as from each plant, the result was the same—a distinct majority of the hoary form.

Experiments 75—77 give the corresponding results when each successive cross was made with a recessive parent of a different flower-colour $(DR_1 \times R_2) \times R_3$. Here the offspring were almost all of the dominant form, only a single individual giving the expected result 1D : 1R. From the rest taken together, three recessives alone were obtained out of a total offspring of 397. Now two of the three seed parents which gave the result in Experiment 77 gave a Mendelian result in Experiment 73, and three out of the eight plants used in Experiment 75 were among those used in Experiment 72; moreover, the same pollen parents were used in Experiments 69, 71, 73 as in Experiments 75 and 76; and again in Experiments 70 and 74 as in Experiments 72 and 77.

Table IX.—Offspring obtained from $[(D \times R_1) \times R_2]$.

a. When the seed parent is hoary and is crossed with R_2.
b. ,, ,, ,, ,, ,, ,, R_3.
c. ,, ,, ,, glabrous ,, ,, R_2 or R_3.
d. ,, ,, ,, hoary ,, self-fertilised.

Number of experiment.	Parentage.	Number of seed plants.	Number of flowers.	Number of offspring.		Expected result.
				Hoary.	Glabrous.	
	a.					
69	$[(2 \times 5c) \times (5a \times \text{self})] \times [(5a \times \text{self}) \times \text{self}]$	4	9	97	106	1D : 1R.
70	$[(2 \times 5c) \times (5b \times \text{self})] \times [(5b \times \text{self}) \times \text{self}]$	4	8	138	138	,,
71	$[(3a \times 5c) \times (5a \times \text{self})] \times [(5a \times \text{self}) \times \text{self}]$	3	8	77	94	,,
72	$[(3a \times 5c) \times (5b \times \text{self})] \times [(5b \times \text{self}) \times \text{self}]$	5	7	114	57	,,
73*a*	$[(3b \times 5c) \times (5a \times \text{self})] \times [(5a \times \text{self}) \times \text{self}]$	7 (purple flowered)	10	133	131	,,
73*b*		1 (red flowered)	2	21	—	,,
74	$[(3b \times 5c) \times (5b \times \text{self})] \times [(5b \times \text{self}) \times \text{self}]$	1	1	19	21	,,
	b.					
75	$[(3a \times 5c) \times (5b \times \text{self})] \times [(5a \times \text{self}) \times \text{self}]$	8	10	335	2	,,
76*a*	$[(3b \times 5c) \times (5b \times \text{self})] \times [(5a \times \text{self}) \times \text{self}]$	1	2	27	—	,,
76*b*		1	1	24	23	,,
77	$[(3b \times 5c) \times (5a \times \text{self})] \times [(5b \times \text{self}) \times \text{self}]$	3	3	32	1	,,
	c.					
78	$[(2 \times 5c) \times (5b \times \text{self})] \times [(5b \times \text{self}) \times \text{self}]$	3	6	—	163	All R.
79	$[(3b \times 5c) \times (5a \times \text{self})] \times [(5a \times \text{self}) \times \text{self}]$	2	3	77	1	,,
80	$[(3b \times 5c) \times (5a \times \text{self})] \times [(5b \times \text{self}) \times \text{self}]$	1	1	17	—	,,
	d.					
81	$[(3a \times 5c) \times (5a \times \text{self})] \times \text{self}$	2	10	140	89	3D : 1R, or all D, according as $[(D \times R_1) \times R_2]$ was DR or D.
82	$[(3a \times 5c) \times (5b \times \text{self})] \times \text{self}$	7	30	250	118	
83	$[(3b \times 5c) \times (5a \times \text{self})] \times \text{self}$	3	several	146	65	
84	$[(3b \times 5c) \times (5b \times \text{self})] \times \text{self}$	2	9	119	41	

Otherwise expressed:—

Individuals used as ♀s ……… {
in Experiment 73 gave a Mendelian result when crossed with R_2.
in Experiment 77 gave an aberrant result when crossed with R_3.

also

Individual recessives used as ♂s in the third pollination {
in Experiments 69, 71, 73 gave a Mendelian result.
in Experiments 75 and 76 gave an aberrant result.
also
in Experiments 70 and 74 gave a Mendelian result.
in Experiment 77 gave an aberrant result.

Therefore the difference between the results can scarcely be attributed merely to the individual constitutions of either parent, but must be due to some relation subsisting between the two.

The fewness of recessives occurring among the offspring in the $(DR_1 \times R_2) \times R_3$ unions as compared with those obtained from the $(DR_1 \times R_2) \times R_2$ unions, recalls the results obtained in the second generation, where the same DR cross-bred plant was found to give varying proportions of recessive offspring according to the particular R form with which it was next crossed, and confirms the observation then made, that *the order in which the recessive forms are used* seems to have an effect in determining the proportion of hoary and glabrous offspring. The fact nevertheless remains, that the only visible difference between the successive glabrous pollen parents was in colour.

In regard to the seed-colours, which are omitted from the accompanying table (Table IX), there was sometimes diversity, sometimes uniformity, but in any given union, either the one condition or the other usually prevailed in all matings.

The seed-colour was sometimes correlated with the leaf-character and sometimes not. When correlation occurred, brown seeds produced glabrous plants, and green seeds hoary plants; the intermediates were too few to allow of any generalisation.

Such correlation was observed in Experiments 69 and 71, with the exception of four seeds (which possibly were wrongly classified); in Experiment 73 (another repeated cross with the white-flowered 5*a*) in six out of the seven matings giving the Mendelian result; also probably in Experiments 75 and 77 (an alternate cross with white- and cream-flowered recessives). In Experiments 70, 72, and 74 (a repeated cross with a cream-flowered recessive), and in Experiment 76, the seeds were not easily classified in regard to colour.

As regards Experiments 78—80, where the final seed parent was glabrous, we have a normal Mendelian case in 78, the offspring being all glabrous. But in 79 and 80 the result is puzzling and entirely inexplicable upon the Mendelian theory, for these two unions between plants of the recessive form gave offspring which, with a solitary exception, *were all dominants.* It may be added that the two final seed parents from which this unexpected result was obtained were sister plants to the exceptional individual previously mentioned in Experiment 73 as having given *all dominants* when crossed with a recessive. (See Conclusions, p. 86.)

The three exceptional plants arose from a cross between a cross-bred and an individual pure recessive (5*a*) which was used as pollen parent in several parallel experiments giving normal results. That cross gave both green and brown seeds, the three exceptional plants (one hoary and two glabrous) all arising from the latter. Sister plants arising from the green seeds were all hoary, and three of them contributed to the Mendelian result in Experiment 73.

Fortunately the two exceptional glabrous plants were also self-fertilised, and the result in this case was precisely the same as in all other cases of self-fertilisation of individuals of the recessive form—the offspring were all glabrous (see p. 79). But for this result one might have been tempted to suppose that some error had occurred in recording the leaf-character in these two plants. It seems equally improbable that in the final cross any such mistake as the unintentional taking of pollen from a hoary individual similar in colour to the recorded glabrous parent can have been made. Such an explanation would still leave the result in Experiment 80 unexplained, since at the time that this experiment was made, no *cream*-flowered *hoary* plants had ever been seen. These two cases, then, remain as the solitary instances among all the various unions that were made, of the occurrence of *dominant* offspring when both parents belong to a *recessive* type.

The results of Experiments 81—84, in which hoary cross-breds of the form ($DR_1 \times R_2$) were self-fertilised, are on the whole confirmatory of those obtained from the self-fertilisation of the (DR_1) cross-breds from which they were derived. In the two cases in which the dominant ancestor was the hoary form 3*a* (Experiments 81, 82), the proportion of recessive offspring obtained from the ($DR_1 \times R_2$) cross-breds was, as in the case of the (DR_1) cross-breds, considerably in excess of the theoretical result 3D : 1R. When 3*b* was employed as the dominant parent in place of 3*a* (Experiments 83, 84), we get a Mendelian result (3D : 1R) from two cross-breds of the form [(3*b* × 5*c*) × 5*b*], as we did from their cross-bred ancestors (3*b* × 5*c*). On the other hand, from two of the three cross-breds of the form $[(3b \times 5c) \times 5a]$, which contributed to the total result 146D 65R (in Experiment 84), the proportion of recessives is a good deal too high.

2. *Offspring of Cross-breds produced from* $(R \times D)$.

a. *When the Cross-breds were Fertilised with a Recessive Form* (*Table X*).

α. In Experiment 85, in which the cross-breds $(5a \times 1)$ were crossed with a recessive of the same type as the recessive parent 5*a*, every fruit contained green and brown seeds in very varying proportions, and usually a few intermediates. All the intermediates (16) were sown, and glabrous plants only were obtained from them; samples of green and brown seeds gave all hoary (33) and all glabrous (16) plants respectively. Correlation between leaf-surface and seed-colour was apparently complete. On the assumption that all the green seeds would have produced hoary plants, and all those not green, glabrous plants, the offspring from every fruit would have been mixed, and the total numbers would have been in the proportion 228 hoary and 191 glabrous, as compared with the expected result 1D : 1R.

In Experiment 86, in which the cross-breds $(5b \times 1)$ were crossed with a recessive of the same type as the recessive parent 5*b*, every fruit contained seeds of the three colours. None of the colours were strictly correlated with either leaf-character, hoary plants being obtained from almost all the green, most of the intermediate, and some of the brown seeds. It was therefore necessary to make full sowings, in order to ascertain the relative numbers of the two leaf-characters: 297 hoary and 302 glabrous plants were obtained.

In both these experiments, 85 and 86, the recessive forms successively employed were alike in flower-colour, and in both it will be noticed that the results are in agreement with Mendel's ratio.

In the four following experiments (87—90), in which R_1 and R_2 were of different flower-colour, and both brown in seed-colour, we see the same more or less complete disappearance of the glabrous form which has already been noted in Experiments 60, 63, 75, 77, although some of the seed parents employed, *e.g.*, in Experiment 87, were the same as those which gave normal results in Experiment 85. In two cases (Experiments 87, 88) in which the seeds were of mixed colours, there was some degree of correlation between seed-colour and leaf-character, the few glabrous plants that were obtained being all derived from brown and intermediate seeds. In a third case (Experiment 90) no such correlation occurred; green, brown, and intermediate seeds alike yielded hoary plants only. In the remaining case (Experiment 89) in which the seeds were all green, the offspring obtained from a sample sowing were again exclusively hoary.

In Experiment 91, in which R_1 and R_2, unlike in flower-colour, were both *green* in seed-colour, green and intermediate coloured seeds were produced, but not brown. Both occurred in every fruit, and both gave rise to hoary and glabrous plants, the totals in the case of both seeds and plants being fairly consistent with Mendel's ratio (82 green, 70 intermediate : 64 hoary, 76 glabrous).

These remarkable results are in harmony with those obtained from the (D × R) cross-breds (Table VI), and show that when the same recessive strain is introduced in each successive cross, Mendel's law holds; but that the successive use of recessive strains of different colour may exert some disturbing effect upon the numerical relation of the two kinds of offspring—an effect of which the data at present to hand afford no explanation. (See Conclusions, p. 86.)

b. *Offspring obtained when the Cross-breds were Self-fertilised.*

In Experiment 92 (Table XI) the cross-breds ($5a \times 1$), of which several were among the number of those previously used for Experiments 85, 87, were self-fertilised. Every cross-bred produced green, brown, and intermediate seeds, the proportion of green to non-green being roughly 3 : 1, except in one mating, in which only one fruit was gathered. Sample sowings showed complete correlation between seed-colour and leaf-characrer, green seeds giving rise to hoary, brown and intermediate to glabrous plants. Presumably, therefore, the total number of plants would have been in the proportion 1244 hoary and 407 glabrous—a very close approximation to the Mendelian ratio 3 : 1.

In Experiment 93 cross-breds ($5b \times 1$), several of which had been previously used for Experiments 86 and 88, were self-fertilised. The resulting seeds were mixed, but in very varying proportions. The number of intermediates was large—nearly one-fourth of the total number. Of the samples sown, green seeds again produced hoary plants; brown seeds, with four exceptions, glabrous plants, unless these four seeds should more properly have been included among the intermediates. The intermediates, however, yielded both forms, and it was therefore necessary to sow the whole number. Unfortunately, a large proportion—more than 100—failed to germinate. If, however, we may suppose that no considerable error is due to this fact, then, assuming perfect correlation in the case of the two other colours (four seeds excepted), the total number of plants would have been in the proportion 1429 hoary, 373 glabrous, or as 3·8 : 1.

In each of the three following experiments (94—96) only a single cross-bred was self-fertilised. The seeds were difficult to sort, and a full sowing was therefore necessary. In the case of the cross-bred ($5d \times 1$) (Experiment 94), an exact Mendelian result was obtained (117D, 39R). With the cross-breds ($5e \times 1$) and ($6c \times 1$), however, the numbers showed a considerable deviation from the expected result—98 D to 18 R in the former case, 175D to 39R in the latter.

TABLE X.—Offspring obtained from Fertilising the Cross-breds (R × D) with a Recessive Form.

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
85	(5*a* × 1) × (5*a* × self) (*G.wh.br.* × *H.wh.bl.*) × *G.wh.br.*	1	2	60	3	43	*gr.* 21 — —	— *in.* 3 *br.* 11	Purple.	White.
		1	1	25 (12 sown)	1	12 (5 sown)	*gr.* 12 — —	— *in.* 1 *br.* 5		
		1	1	30	5	29	— — —	— *in.* 5 —		
		1	1	38	2	21	— — —	— *in.* 2 —		
		1	1	39	2	18	— — —	— *in.* 2 —		
		1	1	19	—	43	— — —	— — —		
		1	1	17	3	9	— — —	— *in.* 3 —		
	Total............	7	8	228	16	175	33	32		

86	(5*b* × 1) × (5*b* × self)	1	3	75	31	42				
	(*G.cr.br.* × *H.wh.bl.*) × *G.cr.br.*	1	5	51	82	51	*gr.* 5 *in.* 14 *br.* 12	*gr.* 3 — *br.* 22	Purple, red	Cream, white.
		1	3	77	51	76	*gr.* 37 *in.* 27 *br.* 10	— *in.* 15 *br.* 65	Red	Cream, white.
		1	2	41	34	59	*gr.* 8 *in.* 28 —	— *in.* 5 *br.* 53		
		1	2	48	39	65	*gr.* 39 *in.* 21 *br.* 28	— *in.* 4 *br.* 52		
		1	2	49	46	44	*gr.* 25 *in.* 31 *br.* 1	— *in.* 9 *br.* 43	Purple.	
		1	1	19	15	29	*gr.* 19 *in.* 12 —	— *in.* 3 *br.* 28	Purple.	Cream, white. Cream, white.
	Total............	7	18	360	298	366	297	302		
87	(5*a* × 1) × (5*b* × self)	1	2	97	—	—				
		1	1	58	—	—	*gr.* 40	—		
	(*G.wh.br.* × *H.wh.bl.*) × *G.cr.br.*	1	1	56	—	—	*gr.* 47	—		
		1	1	57 (12 sown)			*gr.* 11	—		
					1	6	— —	*in.* 1 *br.* 1	Purple.	White. White.
	Total............	4	5	268	1	6	98	2		
88	(5*b* × 1) × (5*a* × self)	9	13	∞ (98 sown)			*gr.* 73	—	Purple (various).	
	(*G.cr.br.* × *H.wh.bl.*) × *G.wh.br.*				7	2	*in.* 5 —	*in.* 1 *br.* 2		White.
	Total............	9	13	∞	7	2	78	3		

Table X—*continued.*

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
89	(5*c* × 1) × (5*a* × self) (*G.r.br.* × *H.wh.bl.*) × *G.wh.br.*	1	2	101 (24 sown)	—	—	23	—	Purple.	
90	(5*d* × 1) × 5*b* × self) (*G.pk.wh.br.* × *H.wh.bl.*) × *G.cr.br.*	1	1	12	19	17	*gr.* 1 *in.* 11 *br.* 17	— — —		
		1	3	60	22	85	*gr.* 14 *in.* 18 *br.* 21	— — —		
	Total............	2	4	72	41	102	82	—		
91	(6*d* × 3*a*) × (6*c* × self) (*G.li.gr.* × *H.wh.br.*) × *G.cl.gr.*	1	2	43	24		*gr.* 21 *in.* 9	*gr.* 17 *in.* 15	Purple (various) White, pinkish-white	Purple (various). White, pinkish-white.
		1	1	12	9		*gr.* 4 *in.* 2	*gr.* 8 *in.* 7		
		1	1	18	22		*gr.* 10 *in.* 9	*gr.* 4 *in.* 12		
		1	1	9	15		*gr.* 3 *in.* 6	*gr.* 5 *in.* 8		
	Total............	4	5	82	70	—	64	76		

Table XI.—Offspring obtained from the Self-fertilisation of hoary Cross-breds (R × D).

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
92	(5*a* × 1) × self (*G.wh.br.* × *H.wh.bl.*)	1	6	270	26	57	—	*in.* 16		
		1	3	152	3	41	—	*in.* 3		
		1	1	58	2	5	—	*in.* 1		
		1	1	47	3	11	—	*in.* 1		
		1	3	139	9	32	—	*in.* 5		
		1	5	229	15	71	—	*in.* 11		
		1	4	177	12	54				
		1	4	172 (59 sown)	6	60 (32 sown)	*gr.* 59 — —	— *in.* 5 *br.* 32	Purple.	White.
	Total........	8	27	1244	76	331	59	74		

Table XI—*continued.*

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
93	$(5b \times 1) \times$ self	1	1	35 (12 sown)			*gr.* 12	—	Purple.	
	(*G.cr.br.* × *H.wh.bl.*)				13		*in.* 8	*in.* 2		
						16	*br.* 1	*br.* 10		Cream, white.
			?	153 (12 sown)			*gr.* 10	—	Purple.	
					46		*in.* 25	*in.* 1		
						54 (12 sown)	—	*br.* 11		Cream, white.
		1	1	43 (12 sown)			*gr.* 10	—	Purple, except 1 pink.	
					25		*in.* 12	*in.* 7		White.
						—	—	—		
		1	?	134 (12 sown)			*gr.* 12	—	Purple.	
					44		*in.* 29	—		
						65 (12 sown)	—	*br.* 11		White.
			1	40						
					23		*in.* 15	*in.* 6		
						9	—	*br.* 9		
		1	1	34						
					20		*in.* 14	*in.* 2		
						11	—	*br.* 10		
		1	1	56						
					13		*in.* 11	—		
						8				

		1	1	47	19	7	*in.* 13	*in.* 4		
		1	1	38	20	11	*in.* 17 *br.* 1	— *br.* 10		
		1	4	168	86	30	*in.* 44	*in.* 8		
		1	1	37	14	14	*in.* 10 —	*in.* 5 *br.* 14		
		1	2	72	30	24	*in.* 26	—		
		1	1	47	5	17	*in.* 1 *br.* 2	— *br.* 7		
		1	1	34	27	16	*in.* 13	*in.* 3		
		1	2	77	28	21	*in.* 16	*in.* 2		
		1	1	34	19	18	*in.* 1	—		
	Total..........	14	19	1049	432	321	317	122		
94	(5*d* × 1) × self (*G.pk.wh.br.* × *H.wh.bl.*)	1	?	Not classified			117	39	Purple	White.
95	(5*e* × 1) × self (*G.bl.pk.br.* × *H.wh.bl.*)	1	?	,, ,,			98	18	Purple, white	Purple, white.

Table XI—*continued.*

No. of expt.	Parentage.	No. of seed parents.	No. of flowers.	Colour of resulting seeds.			No. of offspring.		Colour of corolla in offspring.	
				Green.	Inter.	Brown.	Hoary.	Glabrous.	Hoary.	Glabrous.
96	(6*c* × 1) × self (*G.cl.gr.* × *H.wh.bl.*)	1	?	Not classified.			175	39	Purple, white, pink	Purple, white, pink.
97	(6*c* × 3*a*) × self (*G.cl.gr.* × *H.wh.br.*)	1	1	32		8	*gr.* 20 *br.* 6	*gr.* 9 *br.* 2	Pink, bluish-pink White	Pink, bluish-pink. White.
		1	1	30		12	*gr.* 20 *br.* 7	*gr.* 10 *br.* 4		
	Total..........	2	2	62	—	20	53	25		

In Experiment 97, in which the cross-breds ($6c \times 3a$) were self-fertilised, green and brown seeds were obtained in the proportion of 3 to 1. There was no correlation between seed-colour and leaf-character, for each colour gave rise to both kinds of plants. The totals 53D and 25R show too high a proportion of the glabrous form, a result which entirely agrees with that obtained from the self-fertilisation of the other set of cross-breds in which the hoary type $3a$ was used as the dominant parent (Experiment 67).

From (R × D) × self, therefore, close Mendelian results were obtained in three out of the five cases in which the D parent was of the hoary type 1, viz., in those in which the R parent had white, cream, or pinkish-white flowers; but when the R parent had bluish-pink or claret-coloured flowers, there was a deficiency of R offspring. On the other hand, when the type $3a$ was used as the D parent, there was too high a proportion of R plants.

c. *Offspring of Dominant Cross-breds produced in 2a* (*Tables XII and XIII*).

In accordance with the Mendelian hypothesis, all dominant cross-breds resulting from the cross (R × D) × R, are of the class of impure dominants, and when self-fertilised, yield D and R in the proportion of 3 to 1. We should therefore expect all the final seed parents in Experiments 98—102 (Table XII) to yield a mixed offspring in which the proportion of hoary to glabrous is as 3 to 1. On the other hand, dominants resulting from (R × D) × self are by theory of *two* kinds—(1) impure dominants as above, and (2) pure dominants, which, when self-fertilised, yield dominants and dominants only. In Experiments 103—107 (Table XIII) we should therefore expect the results to vary, according as the final seed-parents selected at random belonged to the former or the latter class.

In Experiments 98 and 99, in which cross-breds of the form $[(R_1 \times D) \times R_1]$ were self-fertilised, there is close agreement between the observed and the theoretical result, 3D : 1R.

In Experiments 100—102 (Table XII), in which cross-breds of the form $[(R_1 \times D) \times R_2]$ were self-fertilised, we find that some of the cross-breds give the expected result 3D : 1R; others on the contrary yielded *only dominants.*

This fact is the more surprising since such cross-breds giving one a Mendelian and another an aberrant result, may be sister plants, derived by self-fertilisation from the same parent.

In Experiments 103—107, in which fourteen individuals selected at random from among the dominant offspring of various self-fertilised (R × D) cross-breds were self-fertilised, eight were evidently pure dominants, and produced only dominants, six were impure dominants,

Table XII.—Offspring obtained by Self-fertilisation of [(R × D) × R] when it is Hoary.

Number of experiment.	Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.		Expected result.
				Hoary.	Glabrous.	
98	[(5*a* × 1) × (5*a* × self)] × self	2	18	298	95	3D : 1R.
99	[(5*b* × 1) × (5*b* × self)] × self	3	12	364	113	
100*a*	[(5*a* × 1) × (5*b* × self)] × self	1	?	105	—	
100*b*		1	?	73	29	
101	[(5*b* × 1) × (5*a* × self)] × self	3	24	348	110	
102*a*	[(6*d* × 3*a*) × (6*c* × self)] × self	1	5	94	—	
102*b*		2	5	68	17	

Table XIII.—Offspring obtained by Self-fertilisation of [(R × D) × self] when it is Hoary.

Number of experiment.	Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.		Expected result.
				Hoary.	Glabrous.	
103*a*	[(5*a* × 1) × self] × self	4	12 or more	374	141	3D : 1R. or all D, according as [(R × D) × self] was DR or D.
103*b*		3	8 or more	372	—	
104	[(5*b* × 1) × self] × self	1	12	190	—	
105	[(5*d* × 1) × self] × self	1	2	101	—	
106*a*	[(5*e* × 1) × self] × self	2	2	12	3	
106*b*		1	1	48	—	
107*a*	[(6*c* × 1) × self] × self	1	4	63	14	
107*b*		1	8	70	—	

and yielded a mixed offspring, in one experiment 374D, 141R, in the second 12D, 3R, and in the third, 62D, 14R.

d. *When the Cross-breds were Fertilised with a Dominant Form.*

When some of the various (R × D) cross-breds used in the preceding experiments were crossed with the same hoary white-flowered Brompton Stocks, (7*a* and 7*b*), used in the experiments described in Table II, the resulting offspring (148) were, in accordance with expectation, all hoary.

III. *Purity of "Extracted" Recessives and Dominants.*

According to the Mendelian hypothesis, such recessives are pure, and should behave as though they were of unmixed descent. If this be the case, they should, when self-fertilised, produce recessives and recessives only. To test this particular point, many such extracted recessives were self-fertilised, and thus produced more than 1000 offspring, all of which were recessive, so far confirming the anticipation as to their purity.

At the same time we have the contradictory result mentioned in Experiments 79 and 80, that from two such extracted recessives crossed with a *pure* recessive (the product of two generations of self-fertilisation), 94 *dominants were obtained and a single recessive.* This result is unexplained.

Purity of extracted *Dominants* was shown in Experiments 103*b*, 104, 105, 106*b*, 107*b*.

IV. *Nature of Recessives produced in the First Crosses.*

These first-cross recessives, when self-fertilised for two generations, invariably gave recessive offspring, having flower- and seed-colours identical with those of the original glabrous parent. The number thus produced, by several individuals, amounted to more than 200 in the first generation and about 130 in the second.

The question whether such recessives can have been the result of accidental self-fertilisation was considered (p. 44), and at present we strongly incline to think that they were not, while fully recognising the difficulties this view entails.

V. *Time of Flowering of Cross-breds.*

Of the original types, some were annual, some biennial.

Only a limited number of observations were made upon the inheritance of these qualities, owing to the difficulty of sowing and planting such large numbers simultaneously. The biennial forms (viz., *incana* (type 1), and the various Brompton strains), do not bloom in the first season, but in the second year they usually flower some weeks before the annuals. *With rare exceptions, all cross-bred plants and "extracted" types flowered in the first season.* The offspring of various crosses between annual forms flowered at the same time whether they were hoary or glabrous; but among the offspring of various crosses between hoary biennials and glabrous annuals it was usual for the recessives to flower before the dominants. In fact, the difference in time in some cases was sufficient for the former to be almost over before the latter had well begun. A certain number of these extracted recessives, however, flowered simultaneously with the dominants obtained from the same mating. Very rarely such recessives produced no flowers at all in the first year: in such cases the habit of growth of these plants resembled that of the biennial forms.

VI. *Summary of Conclusions from Experiments with Matthiola.*

The results obtained are so complex that it is difficult to draft statements which shall give a precise and comprehensive view of the phenomena.

Generally speaking, the following rules hold good:—

1. In crosses between hoary and glabrous plants, the former character was dominant, the latter recessive.

2. Such cross-breds, whether self-fertilised, or fertilised with a dominant, or with the original recessive parent, obeyed Mendel's law with fair consistency.

3. Dominant cross-breds, however, fertilised with a recessive *other than the original one*, gave results apparently of two kinds. Some gave the expected Mendelian equality while others gave *all or almost all dominants;* though several such individuals which gave this excess of dominants on fertilisation with a *new* recessive, produced the usual mixture on self-fertilisation. Two individuals, however (Experiments 100*a* and 102*a*), *produced no recessives at all on self-fertilisation* (see p. 77).

4. Similar results (as in 2 and 3), occurred when dominants produced by the second cross with recessives, were again fertilised with recessives.

5. Other notable exceptions to the rule that dominant cross-breds generally fulfil the Mendelian expectation, were seen when two particular types (2 and 3*a*) of hoary plants were used. Type 2 is the "half-hoary" form, but type 3*a* is a fully hoary form. Dominant cross-breds raised from these, when fertilised with *recessives*, gave a Mendelian result; but on self-fertilisation the proportion approaches 1·7D : 1R (calculated from Experiments 51, 66, 67, 97).

6. No plant showing the peculiar feature of the "half-hoary" Type 2 was ever produced as offspring of any of the crosses between the fully hoary and glabrous types, and, indeed, no plant intermediate between these two types ever occurred as the result of such unions.

7. Crosses between the half-hoary type and recessives gave in the first generation fully hoary cross-breds with only two half-hoary exceptions. Of the mixed offspring derived from these fully hoary cross-breds the great majority of dominants were again fully hoary; some, however, were half-hoary, and some intermediate between the half-hoary and the glabrous forms. No line could be drawn between such intermediates and the half-hoary plants, and therefore all are classed together as "intermediate" in the tables. It is possible that the fully hoary cross-breds are DR, and the others DD, but the numbers do not accord well with this simple explanation.

8. Crosses between white-flowered hoary and variously coloured glabrous forms commonly gave purple-flowered offspring (sometimes, however, a blend, *e.g.*, pink from red and white). This fact, and that given in 7, indicate that the first-cross offspring sometimes present atavistic characters. Crosses between different *coloured* pure types were for the most part not made (see p. 46).

9. The results of self-fertilising cross-breds produced by parents of dissimilar colour was usually to reproduce the parental flower-colours, accompanied sometimes by colours not seen in the parents, together with the purple or pink form of the first cross when either occurred.

10. Crosses between parents of different seed-colour, brown and green, showed green to be frequently dominant. Deviations from this general result occurred with certain types used.

11. In certain combinations there was close correlation between (*a*) green colour of seed and hoariness, (*b*) brown colour of seed and glabrousness. *In other combinations, such correlation was entirely wanting.*

12. The rule that plants with flowers, either purple or claret, arose from green seeds was universal. For seed-colours of the pure white types, see pp. 33 and 34.

13. When glabrous plants were produced by the first cross, they were found to be pure recessives, and their colour was that of their recessive parent. Such plants were always the offspring of recessive *seed* parents, and there is therefore suspicion of self-fertilisation. But with the most punctilious care, such recessives repeatedly occurred when certain strains were used, and in crosses with other strains they were uniformly absent.

Taking all evidence together, we incline to believe that these glabrous first-cross offspring were examples of the "false hybridism" of Millardet (see p. 154).

14. The fact stated in 3, that in certain subsequent crosses individuals occurred which were apparently pure dominants, seems to indicate that similar "false hybrids" may occur of pure *dominant* form also.

15. Speaking generally, the results here detailed agree well with those of Correns. But owing to the use of a large number of types,

our results are necessarily much more complex. It should also be noticed that none of our experiments are precisely comparable with that of Correns, who used a biennial hoary type with purple flowers and a biennial glabrous type with flowers "yellowish-white" (or "sulphur-yellow" of Haage and Schmidt). We used no *biennial* glabrous form.

16. In regard to almost every character studied, the behaviour of several of the different types, strains, and even individuals showed special peculiarities.

The reader who has followed the evidence in *Matthiola* will have seen that the phenomena largely conform to the Mendelian principles. Distinct classes of unconformable phenomena occur, and a few quite irregular cases. These several results cannot be adequately presented in a summary, but in the following tables (Tables XIV and XV) an attempt has been made to give a concise statement of the general results obtained from the various experiments.

Of these twelve aberrant cases (Table XIV), nine we may presume were examples of the "false hybridism" of Millardet. For in these unions, contrary to expectation, a mixed offspring was obtained; but the recessive plants, so produced, bred true—all the offspring obtained from them by two generations of self-fertilisation exhibiting the recessive character. Of actually unconformable, and at present unexplained cases, there remain three; viz.:—

One experiment (10) in which two individuals of the half-hoary type, raised by two generations of self-fertilisation, and crossed with a strain of glabrous plants similarly raised, produced offspring which were all R, when the expectation was all D.

And two experiments (79, 80) in which two glabrous individuals (extracted recessives), crossed with two glabrous strains (recessives raised by two generations of self-fertilisation), produced 94 D and 1 R, when the expectation was all R.

The brief summary of results in Table XV shows—

(1) That in the Mendelian cases the deviations from the exact result are sometimes in the one direction (deficiency of D), sometimes in the other (deficiency of R).

(2) That the aberrant cases *where the expectation is* 1 D : 1 R only include a single instance in which there was a successive use of R parents of *similar* flower-colour (one mating in Experiment 73). In all the other aberrant cases the recessive parents successively employed were of *dissimilar* flower-colour.

(3) That *where the expectation is* 3 D : 1 R, the contrast between Mendelian and aberrant cases is less sharp. No wholly consistent grouping of these aberrant cases appears possible, but the following general statements may be made:—

Table XIV.—Unions in which the expectation is an *unmixed* offspring.

Mendelian Cases.

Results obtained when the expectation is all D.			Results obtained when the expectation is all R.		
Reference number of experiment.	Result.	How obtained.	Reference number of experiment.	Result.	How obtained.
1—9, 11—18	1250 D	From various crosses D × R ..	58*c*—*e*, and others not numbered (p. 79)	1148 R	From self-fertilisation of extracted R's.
19, 20*, 21*, 22*, 24, 25, 27—33, 36, 37, 45, and in part 20, 22, 23, 25*, 35, 39, 40, 42, 46	796 D All D (see experiments)	„ „ „ R × D ..	Not numbered (p. 79)	218 R	From self-fertilisation (for one generation) of R's produced in a first cross.
Not numbered (p. 38) ..	148 D	„ „ „ (R × D) × D	Not numbered (p. 79)	113 R	From self-fertilisation (for two generations) of R's produced in a first cross.
56*b*, 103*b* 104, 105, 106*b*, 107*b*	979 D	From self-fertilisation of extracted (presumably pure) D's	58*a*—*b*	639 R	From crossing extracted R's with R's resulting from self-fertilisation.

Aberrant Cases.

When the expectation is all D.			When the expectation is all R.		
Reference number of experiment.	Result.	How obtained.	Reference number of experiment.	Result.	How obtained.
10	72 R	From [(D × self) × self] × [(R × self) × self]	79, 80	94 D 1R	From crossing extracted R's with R's resulting from self-fertilisation.
(In part) 20, 22, 23, 25*, 35, 39, 40, 42, 46	Mixed D and R (see experiments)	From various crosses R × D ..			

Table XV.—Unions in which the expectation is a *mixed* offspring.

Mendelian Cases.

Ratios obtained when the expectation is 1D : 1R.			Ratios obtained when the expectation is 3D : 1R.		
Reference number of expt.	Ratio. D : R.	How obtained.	Reference number of expt.	Ratio. D : R.	How obtained.
85	1·19 : 1	From the cross $(R_1 \times D) \times R_1$	68	2·98 : 1	From self-fertilisation of $(D \times R)$
86	·98 : 1 (neglecting unsown seeds)	" " "	92	3·05 : 1	" " " $(R \times D)$
91	·84 : 1	" " $(R_1 \times D) \times R_2$	93	3·83 : 1	" " " "
49	·99 : 1	" " $(D \times R_1) \times R_2$	94	3·00 : 1	" " " "
50	1·13 : 1	" " "	55	2·92 : 1	" " " $[(D \times R_1) \times R_2]$
59	·86 : 1	" " "	84	2·90 : 1	" " " $[(R_1 \times D) \times R_2]$
65	·94 : 1	" " "	98	3·13 : 1	" " " "
52	1·13 : 1	" " $[(D \times R_1) \times R_2] \times R_2$	99	3·22 : 1	" " " "
53	·85 : 1	" " " "	100*b*	2·51 : 1	" " " "
69	·91 : 1	" " " "	101	3·16 : 1	" " " "
70	1·00 : 1	" " " "	103*a*	2·65 : 1	" " " $[(R \times D) \times \text{self}]$
71	·81 : 1	" " " "	106*a*	4·00 : 1	" " " "
74	·90 : 1	" " " "	? 102*b*	4·00 : 1	
73*a*	1·01 : 1	" " " "			
76*b*	1·04 : 1	" " " "			
? 72	1·00 : 1	" " " "			

Average ratio.......................... 1·03 D : 1R.
Ratio calculated from the sum of the totals.... 1·03 D : 1R.

Average ratio .... 3·18 D : 1R.
Ratio calculated from the sum of the totals.... 3·22 D : 1R.

Table XV—*continued.*

Aberrant Cases.

Results obtained when the expectation is 1D : 1R.			Results obtained when the expectation is 3D : 1R.		
Reference number of expt.	Result.	How obtained.	Reference number of expt.	Result.	How obtained.
87—90	All D or almost all D	From the cross— $(R_1 \times D) \times R_2$	100*a* 102*a*	All D	From self-fertilisation of— $[(R_1 \times D) \times R_2]$
60—63	,, ,, ,,	$(D \times R_1) \times R_2$	51, 54, 56*a*, 66, 67, 81— 83, 97	Offspring mixed ; 1·8D : 1R	$(D \times R)$ in 3 cases $[(R \times D)$ in 1 case$]$ $[(D \times R_1) \times R_2]$ in 4 cases $[(D \times R) \times \text{self}]$ in 1 case
75, 76*a*	,, ,, ,,	$[(D \times R_1) \times R_2] \times R_3$			
73*b*	All D	$[(D \times R_1) \times R_2] \times R_2$	95, 96, 107*a*	,, ,, 4·7D : 1R	$(R \times D)$ in 2 cases $[(R \times D) \times \text{self}]$ in 1 case

(α) That in the two cases in which recessive offspring were altogether absent (Experiments 100*a*, 102*a*), the experiments were of a parallel nature, the dominants in each case arising from the operation $[(R_1 \times D) \times R_2] \times \text{self}$.

(β) That in all such cases (except Experiment 102*a* mentioned in (α)) where the dominant type introduced in the first cross had been one of the annual forms 2, 3*a*, 3*b* (Experiments 51, 54, 66, 67, 81, 82, 83, 97), the proportion of dominants was invariably too low (1·8 D : 1 R). In fact, this aberrant result was universal for all such experiments with the types 2 and 3*a*. Type 3*b*, however, gave a Mendelian result in the two other similar experiments (Experiments 55, 84).

(γ) That in all such cases (except Experiment 100*a* mentioned in (α)), where type 1 had been originally used as a dominant pollen parent, the proportion of dominants was invariably too high (4·73 D : 1 R) (Experiments 95, 96, 107).

[In neither (β) nor (γ) were the operations of precisely the same form as in (α).]

[Note, added March, 1902.

The Aberrant Results obtained from Cross-breds.

Frequent mention has been made of the fact that cross-breds when fertilised with the original recessive, gave Mendelian equality; while when fertilised with a new recessive, they gave all or nearly all dominants. It has been also stated that self-fertilisations in several cases similarly showed the gametes of these individuals to consist of dominants and recessives in the usual proportions.

At first sight it seems impossible to provide a rationale of such cases. One hypothesis, however, suggests itself, which however improbable, is not yet excluded. This suggestion in fact is, that the excess of hoary offspring produced by the cross with the second recessive may actually have been formed by the union of dissimilar gametes, both bearers of the glabrous character. Were this the case, it would be one more example of a "reversionary" form being assumed as a heterozygous character (see p. 144).

The peculiar results obtained in Experiments 73*b*, 79, and 80 are conceivably explicable on the same hypothesis, but it must then be further supposed in those cases that further resolution of the primary character has taken place.

Unfortunately no cross has yet been made between two pure glabrous types, but Messrs. Haage and Schmidt, of Erfurt, have, in reply to questions, most kindly given us their experience in the matter. This is to the effect that crosses between glabrous varieties of *dissimilar* colour may give hoary plants, but very rarely, not more than 1 in 1000 perhaps. In view of their evidence the suggestion here made is exceedingly remote, but some reference to this obvious possibility is called for.

In considering the other aberrant group of cases where cross-breds on self-fertilisation gave too high a proportion of recessives with some consistency, the possibility of "false hybridism" on the recessive side should not be forgotten.]

Part II.—Poultry.

Experiments begun in 1898, *carried out by W. Bateson.*

The two breeds first chosen for experiment were Indian Game and White Leghorn. Experiments were subsequently made with Brown Leghorn, White Dorking, and with a single white Wyandotte hen.

Indian Game are dark birds with yellow legs and pea combs. By a "pea comb" is meant a comb consisting of three fairly regular longitudinal ridges, along each of which are several more or less lumpy tubercles. In both sexes the pea comb is low, that of the cock rising about 1 to 1½ inch from the skull, while that of the hen is only about ¼ to ½ inch high, being in fact rudimentary. In the hen the tubercles may be almost entirely suppressed. Any one who desires to examine such combs can see them any day in a poulterer's shop. From the "single" comb of the Leghorns the pea comb is readily distinguished by the absence of sharp serrations, and by the presence of the lateral ridges (often obliterated in old hens).

In correlation with the low comb, the wattles are also very short, being almost rudimentary in the hen, and only about 1 inch long in the cock. The ear-lobes in both sexes are bright red, like the wattles, but they project very slightly, and though a little full below, they are never pendulous, as in the Leghorn cock.

The plumage of the cock is for the most part black, shot with dark green. The hackles and saddle are broken with a variable amount of dark red, which if noticeable, is considered by the fancier a fault. There is a large brown patch extending across the secondaries.

The plumage of the hen, with the exception of the hackles which are black, is almost entirely composed of black and brown mixed together in almost every feather. The mixture should be in the form called "lacing" (concentric lozenges or rings of colour), which may be either single or double, in the various parts of the body. The quill-feathers are liable to be vermiculated or "mossed" with brown, which is also reckoned a fault.

The details of coloration are complex, but for our purpose need not be described. There is a good deal of variation between strains as regards minor points, but on the whole the breed is a very uniform one.

The down of the newly hatched chicks may be *either* striped dark and light brown, *or* almost entirely without dark stripes, leaving the general colour then a nearly uniform buff. All intermediates may occur, but in individual families there is often a fairly sharp discontinuity in respect of down-coloration, though the birds when grown up may be quite alike.

To the eye, a most striking feature in these birds is the close, "hard" feathering, and upright carriage. It is to the closeness of the feathering that is largely due the appearance of great length of neck and leg, which constitute a prominent character.

The shanks are, in healthy and well-grown birds, of a full deep yellow. In depauperated specimens they are a more dingy yellow.

The bill is either a deep yellow or of a rather dingy horn-colour. Black pigment is not in my experience found in the shanks of pure-bred birds, but there may be a good deal of pigmentation in the bill, especially in cocks.

The eggs are brown, varying in individual birds from a full dark brown to a very pale *café-au-lait*. The colour of the egg varies irregularly with the health of the bird and with the rapidity with which the eggs are being produced, getting paler when eggs follow each other with abnormal rapidity and towards the end of a batch. The number of eggs produced is very small in comparison with most breeds: the hens are good sitters and mothers.

As to the origin of Indian Game I can obtain no certain information. In this country the breed has come into prominence only within the last twenty-five years. It is no doubt closely connected with the Aseel and Malay breeds, but whether it was imported as an already established breed, or whether it has been produced in this country, is not certain. The breed was, and still is, chiefly kept in Devonshire and Cornwall, but now it is widely spread. To those unfamiliar with poultry, it may be mentioned that Indian Game is a breed thoroughly distinct from ordinary Game fowls.

Whatever be its origin, Indian Game breed now as true to their chief characteristics as any other breed. When two pure strains are crossed, the offspring frequently show white patches on the secondaries, and the comb may increase in size,* taking the form here called "intermediate pea." This comb has the three ridges well marked, but the extent upwards from the skull is in the cock about 2 inches, and in the hen about $\frac{3}{4}$ of an inch. The intermediate pea in the cock usually falls over to one side. Such a comb would be considered a great disfigurement, but it certainly may occur in good strains. It should be mentioned that the cocks are generally dubbed for exhibition, and consequently the details of comb structure have not been much attended to by fanciers.

For our purpose it is important to notice that the true pea comb and the intermediate pea are hardly if at all distinguishable *in the newly hatched chick.* The distinction does not become evident, especially in females, until sexual maturity approaches. At all ages both are readily distinguishable from the single comb of the Leghorns.

White Leghorns.

The other breed originally chosen was *White Leghorn.* Leghorns as a definite breed are probably at least 50 years old, and at the present time exist in many colours which breed fairly true. One of the most definite is the white breed, which can be absolutely relied on to propagate itself without notable variation.

The comb is a high single comb, with one row of large serrations of varying number, including at least four or five large points distinct from the more or less irregularly divided anterior and posterior lobes. In the cock the comb is erect. Measured from the skull to the tip of the serration next over the eye, the height in an adult is 3—4 inches, varying in actual size both with age, treatment, and condition. In full-grown cocks it projects forwards over the bill and backwards behind the head, the total length being about 5 inches. Fine prize birds in show condition may considerably exceed these measurements.

In the hen the comb is similar though smaller, usually lying over to one side, the correct position in the fanciers' opinion. The size in hens varies a good deal in individuals, and greatly with condition. About 2 inches high and 3 inches long may be given as average dimensions, greatly exceeded in breeding condition in some cases. In correlation with the high comb, the wattles are long, reaching in the cock to a length of some $4\frac{1}{2}$ inches from the angle of the gape. In the hen they are about 2 inches long. The ear-lobes are bluish or yellowish-white and pendulous, increasing in size greatly with age.

The plumage is entirely white, without the least speck of any colour. It is *never* close-fitting as in Indian Game.

Legs and bill are pale yellow. The older females frequently (? in

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* This has been my experience, but I am not sure if the fact is generally true.

all strains) have large spurs without any decline in fertility. The eggs are white, and produced in great numbers. The hens do not as a rule sit or show any sign of broodiness.

These breeds seemed specially suitable, because they differed from each other in their combs, a structural character. The great apparent difference in proportional length of leg bones, which at first sight seemed capable of measurement, proved on examination to be due almost entirely to the difference in closeness of feathering, the loose feathers of the Leghorns altering the general outline of the body, and making the legs appear shorter by comparison.

A special reason for choosing these two breeds, apart from the general suitability, was that it was possible to obtain birds of each, with a statement as to their immediate pedigree. The stock of Indian Game was supplied by the Rev. E. P. Boys-Smith, vicar of Hordle, Lymington, Hants, who had bred them with care for some years, keeping careful pedigrees. The original White Leghorns came from Mr. E. C. Lister-Kay, of Burley Manor, Ringwood, Hants, and of them also I was given a pedigree, carefully kept though incomplete as regards the individual identity of the hens, several sister hens being run with one cock. Both these gentlemen have supplied many practical hints and information, which have proved most useful.

In the first two years of experiment many troubles occurred, mostly owing to overcrowding and errors arising from inexperience. Consequently the results obtained were on a small scale. A more serious difficulty was caused by the loss of so many chickens in the spring that the thoroughbred strains had largely to be represented by late-hatched birds, a source of difficulty if not actual error, for it is not unlikely that heredity results may differ with health.

List of Original Birds.

The following is a complete list of the birds introduced for the purpose of these experiments, with the abbreviations which will be used hereafter to distinguish them :

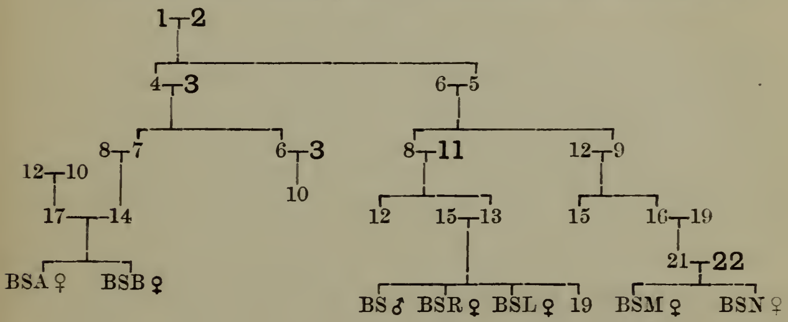
Indian Game.

1. Cockerel and two pullets, own brother and sister, in-bred, from the Rev. E. P. Boys-Smith (BS ♂, BSR ♀, BSL ♀).

2. Two pullets, own sisters, in-bred, related to the above (BSA ♀, BSB ♀).

The above two lots were collaterally related, but showed features of slight difference in colour and build. Both were about equally in-bred. The actual details of the pedigree are complicated, and though little importance may be attached to the details of relationship, I subjoin the pedigree for future reference if required. The extent to which the birds were in-bred may be gathered from the fact that in seven generations only four unrelated birds occur, and the last introduction of fresh blood, or the hen which stands as great-grandmother to one lot and grandmother to the other. The mating generally used was nephew and aunt.

Pedigree of Indian Game Birds received from Mr. Boys-Smith.



In the above pedigree the male is on the left side in each mating. The Clarendon figures show the introduced birds. No doubt all are in some degree related, as the best strains are in few hands.

3. Two hens, full sisters, from Mr. Boys-Smith, sent in 1901, being then in their second breeding season. These are indicated in the pedigree as BSM ♀ and BSN ♀.

4. Cockerel and pullet from the Rev. C. T. Bromwich (Brom. ♂ Brom. ♀). As to the pedigree of these birds, no account was to be had, but it was said that a new male was introduced each year in their immediate pedigree, and the birds bought were almost certainly either full or half brother and sister. As will be seen hereafter, there is doubt as to whether these birds were "pure" in the critical sense.

5. Cockerel of unknown extraction from Ringwood Poultry Farm. (Rd. IG ♂.)

6. Cockerel of unknown pedigree from a Lancashire breeder. (Gr ♂.) The question of true "purity" is also doubtful in this case.

WHITE LEGHORNS.

(*For description see above.*)

1. Cockerel and pullet from Mr. Lister Kay, not in-bred. (LK ♂, LK ♀.)

From a fancier's point of view these birds were not in-bred at all;

for in their pedigree a fresh cockerel, presumably unrelated, was introduced at each successive generation.

2. Cockerel and three pullets hatched from eggs purchased from Mr. Adeane, Babraham Hall (Babr. ♂, Babr. ♀ 42, Babr. ♀ 89, Babr. ♀ 110). These birds were almost certainly not in-bred. They came from a run where many cocks and hens were together, and it is unlikely they were nearly related to each other, though this may have been the case.

3. A pullet from Ringwood Poultry Farm (Rd.L ♀).

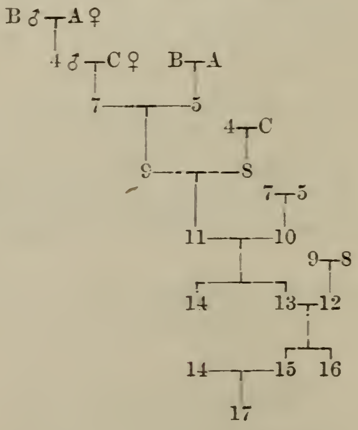
BROWN LEGHORNS.

1. A pullet from Mr. Boys-Smith, sent me in 1900 (Br. L¹).
2. A sister to the foregoing sent in 1901 (Br. L²).
3. A cock sent in 1901, nephew to the foregoing (Br. L ♂).

As regards structural characters, Brown Leghorns closely resemble White Leghorns. In colour of plumage the browns have bright golden-red hackles, red coverts and saddle, with black breast, quills and tails in the cocks, while the hens are of a duller general mottled-brown colour, the hackles being golden yellow, with black central stripe. The breast is a bright chestnut. The deaf ears are white in all Leghorns,* and the bills and shanks are yellow. Eggs white. Hens do not sit. These birds were closely in-bred, as the following pedigree will show:—

Pedigree of Brown Leghorns.

A ♀, B ♂, C ♀ were three unrelated birds.



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* Dr. W. T. Blanford has called my attention to the interesting fact that the *G. bankiva* of Burmah differs from that of India in having the ear-lobes or "deaf ears" red instead of white, and has given me the following references on the subject: Blyth, 'Ibis,' 1867, p. 154, and 'Fauna Brit. India,' "Birds," vol. 4, pp. 76—7.

Here No. 17 represents Br. L ♂, and No. 16 the two hens, Br. L 1 and 2. The usual mating is again aunt and nephew. (Father on the left in each mating.)

WHITE DORKINGS.

The White Dorking is a pure white bird with white bill and shanks, and a *rose-comb*. The feathers are loose-fitting, and never close-fitting. A rose-comb consists of a great number of papilliform elevations, standing in the same horizontal plane. It is wide in the middle, and contracts to a point or "pike" behind.

It is recognisable at an early age in embryonic life, and can never, from about the 9th day of incubation, or earlier, be confused with a single comb. The distinction between rose and single is, with the rarest exceptions, absolute, and no class of intermediates needs here to be distinguished. The rose comb rises about 1¼ inches from the skull in cocks and rather less in hens which are laying, while in hens out of breeding condition, it scarcely rises from the head more than half an inch.

The wattles are about 1½ inches long in cocks, and about 1 inch long in hens. They are rounded in shape. The deaf ears are red and project but little, never being to any extent pendulous.

The bill and shanks are pale pinkish-white, without pigment. The breed has the extra or fifth toe, characteristic of all Dorkings. The eggs are long, of a faint stone-colour, and the hens go broody.

WHITE DORKINGS.

1. Two pullets received from Mr. O. Cresswell, Morney Cross, Hereford, in 1901 (Cr 121 and Cr 122). In Cr 121 a faint tinge of chestnut appeared on one secondary of each wing after the moult of the second year (see p. 98).
2. A cockerel received at the same time from the same source. (Cr ♂.)
3. A pullet received from Miss Knowles, Conholt Park, Andover, in 1900 (K ♀).
4. A cockerel from the same source (K ♂).

From the two birds K ♀ × K ♂ were raised two pullets, Dork. 262 ♀, Dork. 263 ♀, and one cock, Dork. 258 ♂.

Though I have no pedigree with either of these lots, Mr. Cresswell informs me that his birds are very closely bred, but the details are unknown. The breeding of Miss Knowles' birds is also unknown, though in all probability they are not specially in-bred. These two strains are only remotely related. As will appear, it became practically certain later that one (? both) of the K birds was not pure in respect of rose comb. In reply to an inquiry, Miss Knowles was so good as to send information that single combs appear occasionally among her chicks, perhaps 1 in 30, especially when fresh blood is introduced, confirming the view here given. The bearing of these facts will be considered later.

White Wyandotte.

The Wyandotte is another loose-feathered rose-combed breed, but the comb differs from the rose of the Dorking in the fact that the posterior point is directed slightly *downwards* instead of backwards. For our purposes the only other feature of importance is that the deaf ears are round and red, and the bill and shanks yellow. The white variety is not a well-recognised breed, and I know nothing of it beyond the fact that I obtained such a pullet from Ringwood poultry farm. Pedigree unknown.

Before giving the details of specific experiments, it will be useful to state in general terms the results when the various breeds are crossed together. Except in regard to the distribution of pigment in the White Leghorn × Indian Game crosses, reciprocal unions do not differ in result.

Crosses between White Leghorn and Indian Game: General Account.

1. *Comb and Wattles.*—In the cross-bred the comb is almost always *either* a true single comb, frequently but not quite always differing from the pure Leghorn by diminution in size; *or* an intermediate pea. Of the latter there are many degrees.

The distinction between the single and any form of pea comb is *in almost every case* immediately recognisable in the chicks at hatching, and indeed some seven days before. The single comb in unhatched chick lies as a sharply serrated flap of skin folded down on the head, while the pea comb consists of tubercles slightly rising from the skin. In later life the distinction between intermediate and single may become less obvious; but even though the comb may grow up to some height, the three ridges of the pea comb remain marked. The intermediate pea-comb in adults of both sexes usually lies over to one side or the other, like that of the Leghorn hen.

As the sequel shows, the appearance of these two kinds of comb in the first crosses connotes two wholly distinct phenomena; for, while the pea comb is an ordinary dominant DR, the single is a recessive, and *cross-breds with single combs proved incapable of transmitting the pea comb.*

The development of the wattles is closely correlated with that of the comb. Long wattles are associated regularly with a large comb. Owing to the great changes in size to which these structures are subject, according to the state of health, they are not characters suited to very precise measurement.

2. *Plumage-colour.*—Of the hundreds of crosses made both ways, all, with one single exception, were white or dingy white* coloured birds, more or less speckled or "ticked" with black. Such ticking is rarely extensive, and is quite irregular and asymmetrical. The ticking may affect parts of feathers, single feathers, or small patches of feathers.

The ticks may be either plain black, or disposed as barrings or chequerings, especially in hackles and saddle-feathers.† The details of these markings have probably some significance, and may perhaps be described on another occasion.

In addition to the dark ticks the cocks not rarely have patches of reddish or brown colour ("pile") on the wing-covers and saddle rarely as developed as in pile breeds. Such brown marks occur occasionally in hens, but are very small. The brown marks may rarely be barred or chequered.

In respect of ground-colour reciprocal crosses give the same result in *male* offspring. All male cross-breds, and *female* cross-breds *from Indian Game mothers*, have the ground-colour *white*, but *female cross-breds from White Leghorn mothers* almost always have the ground-colour more or less dingy brownish-white. The dinginess is sometimes hardly noticeable, but occasionally it is so striking as to make the bird look a dirty cream colour. It is clearly due to a general deposition of a very fine layer of pigment. Such "dingy" hens, though ticked as the others are with pure black, *never have barred or chequered* feathers, so far as our experiences goes.

In the dingy hens the skin of the face is generally somewhat pigmented, though in various degrees, sometimes approaching to the "purple-face" of Brown-breasted Game and other breeds. No dinginess was ever seen in a male bird.

3. *Bill and Shanks.*—These are full yellow, except in "dingy" hens. In the latter there is pigmentation irregular in amount, varying in the case of the shank from slight patches to a general dark olive. The soles of the feet are always yellow. The bills of dingy hens are striped asymmetrically and irregularly with black or brown. The degree of blackness in shanks is correlated with that in bill fairly closely. This pigmentation begins when maturity is approached and cannot be detected in the shanks of young chicks. Of all the female cross-breds with I.G. fathers which reached the age for pigmentation, only one failed to exhibit it either in bill, or shanks, or in both.

4. *Deaf Ears.*—These are usually patchy, partly red and partly

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* The exception was an extraordinary piebald chick which died young. The middle of the back was occupied by a large irregular island of striped colours, like those of a normal Ind. Game chick. This patch extended asymmetrically on to the proximal parts of the limbs.

† These barred feathers were noticed by Darwin in poultry crosses ('Animals and Plants,' Ed. 2, vol. 2, p. 255), and regarded by him as reversionary.

white, showing a mixture of the parental characters both in colour and shape.

5. *Carriage.*—The attitude of the crosses is much more like I.G. than Leghorn. Though not so "reachy" as a fine Indian Game, they never have the general appearance of Leghorn. This appearance is doubtless due to the fact that the hard, close feathering of the I.G. is always in some degree dominant.

6. *Eggs.*—The shells are usually of intermediate tint. Eggs brown enough or white enough to pass for pure I.G. or pure L. are decidedly rare.

7. *Broodiness.*—Many of the cross-breds became broody and made fair mothers. Some were very uncertain, but perhaps not more so than many hens of sitting breeds. Some did not go broody at all.

In regard to colour of eggs, fertility, and broodiness, for want of opportunities no extensive observations were made.] Moreover, for any adequate study of most of the other points enumerated, it is necessary that the chickens should be reared to maturity. To do this with large numbers is quite beyond our resources. Fortunately, however, the comb-structure can be determined with certainty in very young chicks at about the 14th day of incubation. By the use of this fact the range of available statistics has been greatly increased. For by opening the eggs on the 15th day, the same incubator can be filled more frequently, and the serious expense of raising many hundreds of chickens is so far dispensed with.*

As stated above, the single comb is always single and can be recognised as such from an early stage. Besides variations in size and straightness, single combs sometimes have as a defect one or two lateral processes or "sprigs" at the hinder end. This is a fault to which the best strains are occasionally liable. The pea comb in cross-breds varies greatly as described, ranging through many intermediate forms towards the single comb.

In counting chickens as pea-combed, it will be understood therefore that most of them would undoubtedly have had *intermediate* pea combs on reaching maturity, but none would have had single combs. An attempt was made at first to distinguish pea combs from intermediate pea combs, but this was afterwards abandoned as unreliable. Latterly when the eye became trained, it was fairly easy to

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* When, in these results, the numbers of cases recorded for comb, foot-character, or colour differ, it must be understood that for some reason one or more specimens were only available for certain determinations. For example, a certain number of chicks which died too early (generally about the 10th day) for the comb- or colour-character to be made out with certainty, might show the foot-characters perfectly; in such a case the one character is reckoned and the others are left undetermined. Consequently there is sometimes, as in Experiments 37 and 38, an apparent discrepancy between the numbers given for comb or foot character taken separately, and those given for both in combination.

recognise cross-bred pea combs (DR) from pure peas (DD), at all events in cocks from the first, but the hens are much more difficult.

First Crosses between Brown Leghorn and Indian Game: General Account.

Only a small number of birds of this cross have been reared to maturity, namely, five cocks and eight hens, the offspring of one Brown Leghorn hen and two Indian Game cocks; and one cock bred reciprocally. These cross-bred birds had dark plumage, which may be sufficiently described as compounded of the parental colours and forms: bill, horn colour; legs, yellow; ear-lobes, white tinged with yellow like Leghorn, feathering and carriage intermediate, but nearer to the Game; comb and wattles as in the crosses between Indian Game and White Leghorn.

White Leghorn with White Rose-combed Dorking.

The offspring is always white. The bill and shanks are white like the Dorking, or rarely with a faint tinge of yellow.

In point of carriage and disposition of feathering the two parent forms are so nearly alike, that for our purposes these characters cannot be used as a criterion of inheritance. Deaf ears usually red, or red patched with white, in shape intermediate.

The comb is *either* single as in Leghorn, differing only in reduced height, *or* rose as in the Dorking; but often raised from the head rather more than in the normal form. Wattles follow the comb closely. Some have and some have not the extra toe;* details given later.

As regards characters appearing in later life, such as egg-colour, breeding habits, spurring of hens, &c., the numbers reared to adult life were insufficient to warrant a statement.

In the great majority of cases the extra toe is *either* palpably present as a distinct digit *or* absent. When present the two hind toes may consist, as in the normal Dorking, of a short toe like the hallux of a 4-toed bird, with a long many-jointed digit proximal to it pointing upwards. The two, however, may often be *both* short, pointing downwards, never both long. This condition ranges through many stages of bigemination down to mere bifidity of the nail. A form very rarely seen is an *elongation* of the hallux without any extra toe being present.† In such a hallux there is increase in the number of phalangeal joints. This of course corresponds to the three-jointed pollex in man. More or less complete webbing is common in cross-breds.

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* This foot-character can be sufficiently made out in chicks after about 12 days of incubation.

† [A chick has lately occurred with *such a "long" hallux bigeminus*—probably a hitherto unrecorded form.] March, 1902.

In the highest form of the reduplication the short toe is itself also represented by two digits, making six in all. Of this, also, there are many grades.

Lastly, any of these conditions may be seen on one foot only, while the other foot shows one of the other states or is normally four-toed. Generally speaking, however, there is a fairly close symmetrical agreement between the two feet.

Some of these phenomena have been referred to by many writers,* and a full description could only be given in a separate treatise. For our purposes all the several states indicating digital proliferation in the region of the hallux are counted as "extra toe," inasmuch as they all show the existence of the condition if in varying degrees. When this condition is shown on one foot only, the bird is reckoned with the extra-toed, but the fact is stated.

Brown Leghorn and White Rose-combed Dorking.

Nearly white in general colour of plumage, but with ticks and splashes almost exactly as in the Indian Game—White Leghorn crosses. Otherwise like the White Leghorn—White Dorking crosses.

To the statement in regard to colour the birds bred in Experiment 25 form an exception. Of twenty-two such chicks, four were dark, two were doubtful, and the remainder light. Only two of the darks were reared, and one was like a *dark* Dorking dappled with white, while the other turned out a nondescript brown. It will be remembered that Cr 121 had two chestnut feathers, and must be regarded as, to some extent, DR in point of colour (see pp. 105, 112, and 141).

White Leghorn and White Wyandotte.

Of the latter breed only one hen was used. All her chicks by four different White Leghorn cocks were white birds, slightly ticked in some cases, with yellow legs and bills; having rose combs pointing downwards behind, as in the Wyandotte, though rather higher from the skull; wattles to correspond; deaf ears, reddish patched with white. In general shape like the Wyandotte, laying pale stone-coloured eggs like her, and like her exceptionally fertile. In the pure Wyandotte the eggs should be brownish.

On a survey of the various characters enumerated it at once appears that the distinction between the various kinds of comb, and the distinction in regard to presence or absence of the extra toe, inasmuch as they exhibit a fairly sharp discontinuity, are characters well adapted to statistical treatment. As has also been stated these distinctions can be perceived from an early age in the young chick, so that much larger

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* References in 'Materials for the Study of Variation,' p. 390.

statistics can be obtained in regard to them than as to the other characters. In what follows, therefore, primary regard is had to these characters, though some important considerations arising out of the other characters must also be considered later.

Indication of the Mendelian Laws.—Description of the detailed results may be greatly facilitated if we anticipate the recital of experiments, and state at once that in a considerable group of the crossings the operation of the Mendelian laws can be perceived. This group will be considered first, and for convenience will be referred to as the Mendelian group. Many complications must be dealt with, but so far nothing conflicts with the main result.

The cases grouped as Mendelian all show clear dominance. By speaking of the remainder as non-Mendelian it is not suggested that the heredity is not in accordance with the Mendelian principles; but merely, that as there is a condition more complex than that of simple dominance, the application of the Mendelian principles cannot be clearly followed out.

Using the Indian Game birds of

Sections 1 and 2, and their direct descendants ...	p. 90
Section 3	p. 91
The hen of Section 4	p. 91
The cock of Section 5	p. 91
The Dorkings of Sections 1 and 2	pp. 91 and 92
and the Wyandotte hen	p. 94

with any of the Leghorns, male or female, the facts show that

pea comb,
rose comb,
extra toe[*]

are *dominant* characters, and that

single comb,
the normal foot

are *recessive* characters.

We are thus provided with a terminology and a *rationale* of phenomena, which when we come to the more complex results will be found a valuable guide.

Purity of Strains.—A word must now be said as to the purity of the strains. When the Mendelian principles are appreciated, purity acquires a new and precise meaning. This we shall subsequently discuss (see p. 134). For the present it will suffice to say that in regard to the various Leghorns, we have no evidence of a bird, the offspring of two Leghorns, having a comb other than single or a foot other than four-

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[*] The dominance of this character, as will be seen, is not absolute, and a cross-bred without any trace of extra toe may be DR in respect of that character.

toed. With regard to those characters, therefore, the strains must be called pure.

Similarly the Indian Games and Dorkings, *just enumerated*, have always produced birds with the comb and foot characters* of their respective breeds, so that in respect of these characters they also were pure. Of the actual numbers of thoroughbreds so produced only imperfect records were kept. They would have added to the completeness of this account; but when the results of the crossings are understood it will be seen that these precise numbers would not have contributed anything of significance. In general terms, however, we may say that these numbers were in each case considerable—say from twenty to fifty.

MENDELIAN GROUP.

Crosses between Leghorns and Indian Game.

Details of Experiments in regard to Comb.

The following lists give the actual numbers of birds with each kind of comb obtained by crossing the parents enumerated on p. 99 with Leghorns. The breeding of the Indian Games is stated in the course of the experiments.

By "1 year," "2 years," &c., after the name of the bird is meant that it was in its first or second breeding season, &c. These and subsequent experiments are numbered consecutively for reference.

			P.c.	S.c.
†1.	I.G. BSA ♀ (1 year)	× LK ♂ (1 year)	11	0
2.	„ BSL ♀ (2 years)	× do. (2 years)	9	0
3.	„ BSR ♀ (2 years)	× Babr. ♂ (1 year)	13	0
4.	„ BSB ♀ (2 years)	× do. ♂ (1 year)	7	0

From BSB ♀ (one year) × BS ♂ (one year) were bred the following thoroughbred Indian Games—25 ♀, 35 ♀, and 30 ♂, which, mated with Leghorns, gave the following:

			P.c.	S.c.
5.	Babr. 110 ♀ (1 year)	× I.G. 30 ♂ (2 years)	19	0
6.	Babr. 89 ♀ (1 year)	× do. (1 year)	15	0
7.	BrL1 ♀ (1 year)	× do. (1 year)	19	0
8.	Unknown white Lgh. ♀ bred by us, but label lost	× do. (2 years)	19	0

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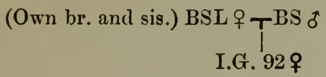
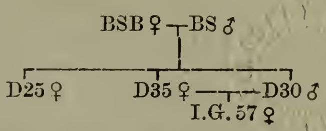
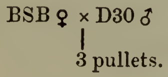
* The extra toes may show occasionally one of the rarer states in these pure-bred birds, but one at least is always present.

† The attempt to cross Legh. LK ♀ with I.G. BS ♂ failed. It was tried repeatedly, sometimes by leaving the two birds for weeks together, at other times putting either in the other's cage. The cock always tore and kicked her, and though he had been kept alone for some days he never trod this particular hen. He was not tried with any other Leghorn.

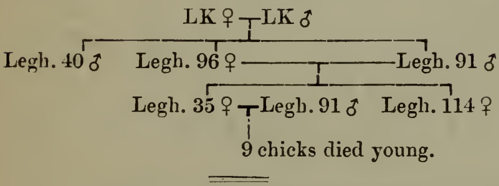
From the original Indian Game of the Mendelian sections, thoroughbreds were raised as follows :

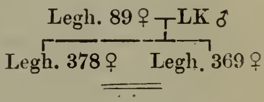


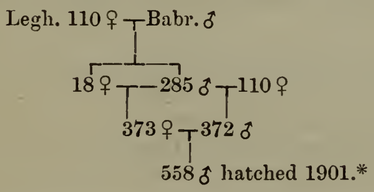


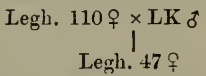


From the original White Leghorns, thoroughbreds were raised as follows :









Using these birds, the following results were obtained :

			P.c.	S.c.
9.	I.G.	35 ♀ (1 year) × Babr. ♂ (1 year)...............	7	0
10.	„	25 ♀ (1 year) × „ (1 year)	4	0
11.	„	57 ♀ (1 year) × Legh. 285 (1 year)...........	6	0
12.	„	3 pullets (BSB ♀ × D30 ♂) × Legh. 355 ♂ (1 year)	12	0

All pullets used in Experiments 9—12, were late-hatched the year before, and consequently laid few eggs, apart from any question of effects of in-breeding.

			P.c.	S.c.
13.	I.G.	92 ♀ (1 year) × LK ♂ (2 years)................	18	1
14.	„	„ (2 years) × 91 (LK × LK)	23	0

From matings 1—14, in some of which the Leghorn was father, in others mother, were produced pea comb 182, single comb 1, so that, with one single exception there was complete dominance of the pea comb.

To these cases of complete dominance we may add the following, in which it must be noticed that Indian Game blood from a new source is introduced. From Indian Game, BSR ♀ × Indian Game Brom. ♂, a

* The numbers in this pedigree are those by which the birds are spoken of.

family was raised of which some were certainly *not* pure in respect of pea combs. For when bred together some, at least, of them were capable of producing, and did produce, single-combed offspring.

This will be fully discussed later, and the relationships of the family tabulated (see p. 112), but at present it may be stated that of this family a pullet and cockerel, own brother and sister, were mated, and produced several chickens, of which two only survived, viz., Indian Game 59 ♂ and Indian Game 120 ♀. Crossed with Leghorns, their offspring were as follows:

	P.c.	S.c.
15. Legh. Babr. 42 ♀ (2 years) × I.G. 59 ♂ (1 year).....	24	0
16. „ „ 89 ♀ (2 years) × „ (1 year).....	17	0
17. Brown Legh. 1 ♀ (2 years) × „ (1 year).....	16	0
18. Legh. 96 ♀ (1 year) × I.G. 59 ♂ (1 year)	24	1 doubtful
19. „ 35 ♀ (2 years) × „ (2 years)...........	15	0
19*a*. I.G. 120 ♀ (1 year) × Legh. LK ♂ (3 years)	7	0

In all, therefore, these two I.G. birds produced 103 p.c., 1 doubtful s.c.

The other Mendelian Indian Game gave the following results:

	P.c.	S.c.
20. I. G. Brom. ♀ (1 year) × Legh. LK ♂ (1 year)	18	0
21. Legh. Babr. 89 ♀ (1 year) × I.G. Rd. ♂ (2 years)	29	1
22. I.G. BSN ♀ (2 years) × Legh. 373 ♂ (1 year)	37	1
22*a*. „ „ (2 years) × Brown Legh. ♂ (2 years)........	34	2
23. „ BSM ♀ (2 years) × Legh. 369 ♂ (1 year)...........	54	0

From these 25 matings, therefore, were produced 457 p.c., 5 s.c., and 1 doubtful.

Crosses between Leghorns and White Dorkings.

Details of Experiments in regard to Comb and Feet. (Mendelian Group.)

	R.c.	S.c.	E.t.	1 e.t.	No e.t.
24. Cr ♀ 121 (1 year) × Legh. 285 ♂ (2 years)	12	0	12		0
25. „ (2 years) × Brown Legh. ♂ (2 years)	22	0	16	4	2
			(see below, p. 113)		
26. Cr ♀ 122 (1 year) × Legh. Babr. ♂	25	1	18		0
27. Legh. 18 ♀ (1 year) × Cr ♂ (1 year).....	23	0	23		0
28. Legh. 96 ♀ (2 years) × „ (2 years)....	20	0	20		0
29. Legh. 47 ♀ (1 year) × „ (1 year)	21	1 inter.*	21	1	0

Taken together, therefore, 2 White Dorking hens with 3 Leghorn cocks gave 59 rose combs and 1 single, while 3 Leghorn hens by the same Dorking cock gave 64 rose combs and 1 doubtful. As regards toe, matings 24 and 26—28 gave 53 birds with extra toe on both sides.

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* This egg was opened at the 14th day, and as the condition could not be clearly made out, it is entered as intermediate. Probably, if it had been reared, it would have been an r.c. The same applies to the "doubtful" in Experiment 18.

Taken together there were—

R.c.	Interm.	S.c.	E.t. both sides.	E.t. one side.	No e.t.
123	1	1	100	5	2

The dominance of the rose comb is therefore almost complete, while that of the extra toe, though very strong, is not quite so complete. Experiment 25 proves that the dominance of the extra toe was distinctly imperfect as against the normal foot of the Brown Leghorn ♂. These results are referred to on p. 113.

White Wyandotte and White Leghorns.

		R.c.	S.c.
30.	Wy. ♀ (1 year) × Legh. Babr. ♂ (1 year)	17	0
31.	,, (2 years) × ,, LK ♂ (3 years)	5	0
32.	,, (1 year) × ,, 40 ♂ (1 year)	3	0
33.	,, (2 years) × ,, 91 ♂ (1 year).........	20	0

In all, therefore, this hen produced 45 rose combed chicks by four cocks and no single comb.* All the chicks reared were white, or white with a few ticks of black, barred in several. The general shape agreed nearly with the Wyandotte: legs and bill yellow, ear-lobes red patched with white.

Experiments 1—33, therefore, show that the pea comb, rose comb, and extra toe are in certain strains dominant almost without exception. A distinct departure from this regular dominance as regards toe is seen in Experiment 25 (see p. 113).

First Crosses bred together.

34. From Experiment 17, Brown Leghorn 1 ♀, by Indian Game 59 ♂, 4 pullets and 1 cockerel were taken, and their eggs incubated through the whole breeding season of 1901.

They gave 166 pea combs and 59 single-combs, or 2·8 : 1. All the chicks were more or less dark on hatching. Those that were lightest were buff but had dark quills showing, so that there is no doubt they would all have proved dark birds.

35. The cock (dark; pea comb) used in Experiment 34 was put with 5 hens (light; pea comb), viz., 3 that had been used in Experiment 36, 1 bred in Experiment 14, and 1 bred in Experiment 5. This was at the end of the season, 1901, when most hens had stopped laying. It was not known which hens laid the eggs, but they gave collectively 19 p.c. and 6 s.c., or 3·1 : 1.

The colour-result was altogether *contrary* to simple expectation on

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* Mr. Grosvenor Berry informs us that in crosses he has made with Golden Wyandotte, the rose comb was always dominant, without exception, over single comb.

the hypothesis that the colorations of Brown Leghorn and Indian Game can be treated as both alike "dark." The chicks were nineteen dark and six light, whereas equality would be expected on the above hypothesis. [See note, p. 141.]

36. From Experiment 17 (Leghorn Babr. 42 ♀ × Indian Game 59 ♂) four pullets and one cockerel were similarly bred together for the season, 1901, with the result 147 pea comb, and 45 single comb, or 3·27 : 1.

In this case the grandparents were of strikingly different colours, white and dark respectively, and as has been said the first crosses in these matings are light birds. Taken broadly, therefore, *light* is here dominant, and dark is recessive, and, as a matter of fact, the offspring of Experiment 36 consisted of 149 light, and 41 dark, or 3·6 : 1, a proportion not greatly removed from 3 : 1.

Grouped according to both characters, comb and colour, the offspring were—

Light with pea comb	111
,, single comb	37
Dark with pea comb	34
,, single comb..................	8

If the numbers followed strictly Mendel's law, they should be a 9 : 3 : 3 : 1.

It must be remembered that here the terms "light" and "dark" each cover several different conditions of plumage, and to this question we shall return, only noting here that adopting this grouping the Mendelian proportions are not very widely departed from (*cf.* p. 109).

37. From Experiment 29, 2 pullets and 1 cockerel were taken and bred together through 1901. They gave 70 rose combs and 13 single combs. These numbers depart very widely from 3 : 1, being in fact, 5·4 : 1. As regards foot they gave 61 chicks with both extra toes, 2 with only 1 extra toe, 22 with no extra toe, thus giving 2·9 : 1. (As to these numbers, see note, p. 140.)

Grouped according to both characters they gave—

R.c. with e.t. (including halves)......	50
R.c. without e.t.	19
S.c. with e.t.	10
S.c. without e.t.	3

There again the numbers should follow 9 : 3 : 3 : 1, from which they considerably depart, owing to the deficiency of recessive combs. We may note that the Mendelian series most nearly fitting these figures are 45 : 15 : 15 : 5.

38. Three pullets and a cockerel from Experiment 24 bred together to end of March, 1901, gave, as regards comb, 85 r.c. and 17 s.c., and as regards toe, 77 with both extra toes, 1 with one extra toe, 29 with

no extra toe. Here also the combs depart widely from 3 : 1, being 5 : 1 (*cf.* Experiment 37), while the toes being 78 : 29, agree precisely, being 3·0 : 1. (As to these numbers, see note, p. 140.)

Grouped according to both characters, they were—

R.c. with e.t.	64
R.c. without e.t.	21
S.c. with e.t.	12
S.c. without e.t.	5

The nearest Mendelian series of numbers is 63 : 21 : 21 : 7.

In this experiment six *dark* chicks (not reared) occurred, though both birds in Experiment 24 were light (see p. 98).

39. At the end of March the cockerel used in Experiment 38 died of tuberculosis, and the cockerel used in Experiment 37 was put to the hens of Experiment 38. On reference to Experiments 24 and 29, it will be seen that the cock was in composition the reciprocal of the hens. As the results of the two experiments were similar, the hens were put to the new cock without an interval, and consequently a few of the chicks here reckoned were doubtless by the first father. At the end of the season also the hens of Experiment 37 were added to those of Experiment 38, and laid about 10 of the chicks here reckoned.

The results were 118 rose combs, 35 single combs; 131 with both extra toes, 28 with no extra toes. The combs are therefore in the ratio 3·3 : 1 and the feet 4·7 : 1.

Grouped according to both characters, there were—

R.c. with e.t.	94
R.c. without e.t.	23
S.c. with e.t.	32
S.c. without e.t.	3

Here there is a considerable deficiency of no e.t. birds. The nearest Mendelian series is 90 : 30 : 30 : 10.

No dark chicks occurred here.

Experiments 37, 38 and 39 together give—

R.c., 273; s.c., 65; or 4·2 : 1
E.t., 272; no e.t., 79; or 3·4 : 1

Grouped according to both characters—

R.c. with e.t.	208
R.c. without e.t	63
S.c. with e.t.	54
S.c. without e.t	11
	336

As was seen in Experiments 37 and 38, the recessive *combs* were deficient, while in Experiment 39 the greater deficiency was in the recessive *feet*. These two deficiencies in this final table partly cancel each other, but as the whole number in Experiment 39 was far greater than in the other two, the table is overweighted by the peculiarity of that family.

In the chief departures from 3 : 1, the near approaches to 5 : 1 should be noticed, viz. :—

In Experiment 37 the combs are	5·4 : 1
,, 38 ,, ,, ...	5·0 : 1
,, 39 the feet are	4·7 : 1

Whether this is a mere coincidence without further significance cannot yet be said.

Wyandotte-Leghorn First Crosses bred together.

40. Four pullets and one cockerel from Experiment 33 bred together until end of July, 1901, gave 196 rose combs and 79 singles, which is approximately only 2·5 : 1. Here the *recessives* for the first time considerably exceed the expected proportion of 1 : 3.

It is a remarkable fact that in this mating a number of *dark* chicks were produced, the numbers being 215 light and 55 dark. But the Wyandotte grandmother, though a white bird without ticks, may for anything known to the contrary have been a cross between a dark and a white bird. If so, her offspring by a White Leghorn, taking white as dominant, would all be light, though consisting of DD and DR birds in equal proportions. It would thus be an even chance that any of the birds used in Experiment 40 were DD or DR. The cock is in any case DR (on this hypothesis). If then one of the hens were DD and the other three DR, the ratio 13D : 3R would be expected, which approaches fairly nearly to 215 : 55. This of course is a mere suggestion; otherwise unsupported.

Several of the results obtained in the foregoing experiments depart considerably from the Mendelian expectations. It is, however, to be remembered that these expectations give average results only. In all cases yet investigated, individuals differ greatly in the results they give, and we can only suppose that these differences represent different proportions in the number of effective dominant and recessive germs which they produce. By putting more than one female in each experiment, we may suppose that cancelling has occurred as betwen the female peculiarities, but as only one male was used at a time, his peculiarities have full scope. For example, the following experiment goes some way towards showing that the aberration of the comb-numbers may be due to this cause.

Dominant First Crosses bred with Pure Recessive.

41. The four pullets used in Experiment 40 after their resting-season were for the remainder of 1901 put with a pure Leghorn cockerel Leg. 369 ♂. They gave 46 r.c. and 50 s.c., or almost equality, which the law demands. All chicks of course light in colour. This experiment was very kindly carried out for me by Mr. R. Assheton, Lecturer on Biology to Guy's Hospital.

42. A similar experiment was made with three dominant first crosses raised respectively in Experiments 5, 15, and 16. Put with a pure Leghorn (355 ♂), for the latter weeks of 1901 they gave—

P.c.	S.c.	Light down.	Dark down.
28	30	57	0

Here again the approach to equality is very close. There are of course no dark coloured chicks, as only one grandparent was coloured.

Nevertheless, that the peculiarity of the male if permanent is not of itself enough to explain the aberrations, is shown by a comparison of Experiments 37 with 38 and 39. In Experiment 37 the same male was used as in Experiment 39, the females being the same in Experiments 38 and 39. But while the feet are practically 3D : 1R in Experiments 37 and 38, they are 4·7 : 1 in Experiment 39. Conversely, while the combs are 3·3 : 1 in Experiment 39, they are about 5 : 1 in the other two experiments. There is at present no obvious explanation of these results, and we can only accept the conclusion that not only different individuals similarly bred may give different proportions, but that these proportions may change also at different times (*cf.*, p. 121).

TOTALS OF MENDELIAN FIRST CROSSES BRED TOGETHER.

Experiments 34—39, added together, give the following totals. Though not strictly legitimate, such promiscuous addition is rendered less objectionable for the reason that in the case of each character which departs considerably from 3 : 1, there are grounds for regarding such a departure as an oscillation and not a departure peculiar to the character.

Pea comb and single comb—

	P.c.	S.c.
Experiment 34............	166	59
,, 35............	19	6
,, 36............	147	45
	332	110 or 3 : 1

Dorking rose comb and single comb—

	R.c.	S.c.
Experiment 37…………	70	13
,, 38…………	85	17
,, 39…………	118	35
	273	65 or 4·2 : 1

Wyandotte rose comb and single comb—

	R.c.	S.c.
Experiment 40…………	196	79 or 2·5 : 1

Dominant combs together 801, and recessives 254, or 3·1 : 1.

Extra toe and no extra toe—

	E.t.	No e.t.
Experiment 37…………	63	22
,, 38…………	78	29
,, 39…………	131	28
	272	79 or 3·4 : 1

Taking combs and feet together there are 1073 : 333, or 3·2 : 1.

Colours.

Plumage.—The case of plumage is a much more complex one, and it is very doubtful if the results on this head should be added to the others at all. As was stated above, first crosses are white, or nearly white, birds. We may therefore regard "light" as dominant against "dark." Moreover, as the colours were in most cases judged on very young chicks, they can only be taken as an indication of down-plumage. But from those that were reared to maturity, it is certain that the "dark" class consists of a number of different kinds of colours, some of which are recurrent and definite, while others are irregular mixtures. At the present time statistics as to these types of coloration cannot be given, though probably another season's work may supply them. An outline of the probable significance of such a series of colorations produced by the first crosses interbred is given under the head of "Compound Allelomorphism." Among the "dark" types produced by the Brown Leghorn-White Dorking first crosses interbred (Experiment 81), were a black form, a cuckoo form, a form like Brown Leghorn spotted with white, female birds of the colour proper to Silver-greys and Duckwings, *i.e.*, white hackle striped with black, grey mottled wings and mantle, with chestnut breast (corresponding male not hitherto seen).

In the "dark" class the Indian Game-White Leghorns (Experiments 36 and 76—80) gave some blacks, some cuckoos, and some nearly approaching Indian Game.

In each case the "light" classes consist of some pure white birds, many white birds flecked with black or red, such as occur in the first crosses; and in the Br. Legh.-Dorking crosses, some white birds with chestnut breasts ("pile").

Until the experiment is completed, no statement can be made, but the opinion may be hazarded that at least some of these colour forms, if corresponding cocks and hens were mated, would breed true from their first appearance (see p. 144).

The Experiments 76—81, from which the colour results are now under discussion, were made with families which were non-Mendelian as regards structural characters, but as regards colour these families were Mendelian in the sense that "light" was dominant against "dark."

Remembering the *caveat* expressed above, taking all cases in which the first crosses between dark and white breeds have been bred together, we have the following results :—

	Light down.	Dark down.
Experiment 36	149	41
,, 76	50	10
,, 77	49	16
,, 78	56	24
,, 79	106	40
,, 80	8	1
,, 81	131	44
	549	176 or 3·1 : 1

Grand Totals.

Adding all dominants and all recessives, we have—

	Dom.	Rec.
Pea comb and single	332	110
Dorking rose comb and single	273	65
Wyandotte rose comb and single	196	79
Extra toe and no extra toe	272	79
Light down and dark down	549	176
	1622	509 or 3·18 : 1

Though this total agrees closely with the expected 3 : 1, it must not be forgotten that several of the observations which contribute to the result show considerable departures from it, and we may suspect that some of these are not merely fortuitous accidents.

For the present also, we do not know that the extracted recessives are pure, or that the dominants consist of pure and crossed, as they may be expected to do, in the proportions of 1 : 2. But taken generally, there is so close an agreement with expectation that these propositions on which the expectation is based, can scarcely be other than at least a fair approximation to the truth.

Colour of Legs.

The colour of legs and bills cannot be safely determined till maturity, and consequently the numbers are too small to warrant a statement of statistical proportions. It may nevertheless be stated that *qualitatively* the offspring of first crosses between White Dorking and the Leghorns agree with the Mendelian expectation. As stated above, such first crosses have whitish legs, but the offspring of the first crosses bred *inter se* have *either* white (including whitish) legs *or* yellow legs.

General Result.

Taking together the structural characters of comb and foot and the colour of legs it appears that each is transmitted independently. As a result, therefore, the several characters may be combined in individuals bred from first crosses *inter se* in any combination, producing, for example, birds with single comb, extra toes and white legs; rose comb, no extra toe and yellow legs, &c., thus fulfilling the Mendelian expectation, though how far the ratios of each combination agrees with that principle, the observations are insufficient to determine.

NON-MENDELIAN GROUP.

We have next to consider a more complex series of results. It has now been shown that in the case of a considerable number of Indian Game, the pea comb is an almost exclusively dominant character as against single comb. Similarly in three White Dorkings the rose comb proved to be a dominant character, and in two of these birds the extra toe was also dominant. In the cases now to be described there was no exclusive dominance, but on the contrary the offspring was always *mixed*, some being pea and some single in the Indian Game crosses, and some rose and some single in the Dorking crosses.

Indian Game and Leghorns giving Mixed Offspring in First Crosses.

In the list of original Indian Game birds there are (1) five closely bred birds of one strain (p. 90, 1 and 2); (2) two hens (p. 91, 3) by a cock of the same strain as (1) out of a hen remotely related. All these birds showed dominance, which was practically exclusive. Of the two birds named in 4 (p. 91) the hen, Brom. ♀, was shown to be exclusively dominant with one Leghorn cock, and the same is the case with regard to the cock Rd. ♂ in 5 (p. 91).

On the contrary, the cock in 4 (p. 91) Brom. ♂ and the cock in 6 (p. 91), Gr. ♂, gave mixed offspring with Leghorn hens, as follows :—

		P.c.	S.c.
43.	Legh. LK ♀ (1 year) × I.G. Brom. ♂ (1 year)	7	18
44.	,, Babr. 42 ♀ (1 year) × I.G. Brom. ♂ (2 years)	10	10
45.	,, Rd. ♀ (1 year) × I.G. Brom. ♂ (2 years) ...	7	5
46.	,, 47 ♀ (1 year) × I.G. Gr. ♂ (1 year)........	14	21
47.	,, 47 ♀ (2 years) and 89 ♀ (3 years) } × I.G. Gr. ♀ (2 years).	15	8
	Of these 5 p.c. and 3 s.c. were laid by 89 ♀ alone after removal of 47 ♀.		
48.	Legh. ♀ (breeding unknown) × I.G. Gr. ♂ (1 year)	8	4
	This hen was used in Experiment 8 (*q.v.*).		

Each mating therefore in which these cocks were used, resulted in a mixture of pea and single, though the proportions vary greatly.

A family (see table, p. 112) of five Indian Game birds were raised from the hen BLR ♀ and Brom. ♂. Of these, three were females, viz., I.G. 17 ♀, I.G. 90 ♀, and I.G. 94 ♀, and two were males, I.G. 12 ♂ and I.G. 15 ♂. Bred with Leghorns these five birds gave mixtures as follows :—

		P.c.	S.c.
49.	I.G. 17 ♀ (1 year) × Babr. ♂ (1 year)	20	16
50.	,, (2 years) × Legh. 285 ♂ (1 year)	16	14
51.	,, (3 years) × Legh. 673 ♂ (1 year)	12	11
52.	I.G. 94 ♀ (1 year) × Legh. 40 ♂ (1 year)	2	8
53.	,, (2 years) × Legh. LK ♂ (2 years)......	15	10
54.	,, (2 years) × Legh. 91 ♂ (1 year)........	9	16
55.	,, (3 years) × Legh. 91 ♂ (2 years).......	4	1
56.	I.G. 90 ♀ (2 years) × ,, (1 year)	6	12
57.	,, (3 years) × ,, (2 years)	6	2
58.	,, (2 years) × Legh. 285 ♂ (1 year)	5	3
59.	,, (3 years) × Brown Legh. ♂ (2 years)...	13	11
60.	Legh. Babr. 89 ♀ (2 years) × I.G. 15 ♂ (2 years)..	8	5
61.	Legh. Babr. 110 ♀ (1 year) × ,, (1 year) ..	12	12
62.	Brown Legh. ♀ Br. L. 1 (1 year) × I.G. 12 ♂ (1 year)	4	8

It is seen, therefore, that each of three hens and two cocks, raised as above, gave mixtures when bred with various Leghorns, and again the proportions of such mixtures vary greatly. Two of these I.G birds, out of BSR ♀ × Brom. ♂, viz., I.G. 90 ♀ and I.G. 12 ♂, were selected, and from them were raised a family of which two only survived. This family consisted of *six chicks with single combs* (see p. 112) and six with pea combs, among which were the two survivors, I.G. 59 ♂ and 120 ♀. The supposed "pure" I.G. birds, therefore, themselves gave a mixture; but the only two survivors, themselves pea-combed, gave exclusively pea-combed offspring, with one doubtful exception only (see Experiments 15—19A).

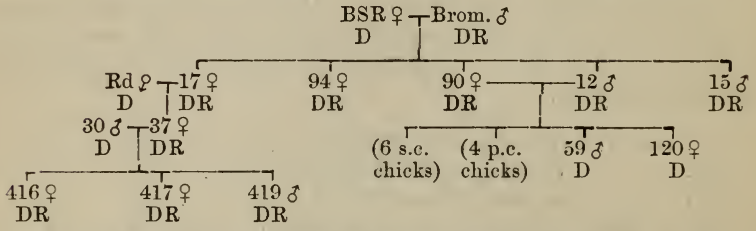
From I.G. 17 ♀ × I.G. Rd. ♂ was produced a family of thirteen chicks, all pea comb. Of these, one, I.G. 37 ♀, was crossed with a Leghorn ♂ as follows:—

		P.c.	S.c.
63.	I.G. 37 ♀ (2 years) × Legh. 373 ♂ (1 year)........	28	29

Previous to the foregoing crosses, I.G. 37 ♀ was bred with I.G. 30 ♂, producing a series of chicks all pea combed, of which two pullets, I.G. 416 ♀ and 417 ♀, and one cockerel I.G. 419 ♂, have been crossed with Leghorns as follows:—

		P.c.	S.c.
64.	Legh. 47 ♀ (2 years) × I.G. 419 ♂ (1 year).......	4	4
65.	„ 96 ♀ (2 years) × „ (1 year).......	11	14
66.	„ 114 ♀ (1 year) × „ (1 year).......	2	5
67.	„ 372 ♀ (1 year) × „ (1 year).......	7	10
68.	I.G. 416 ♀ (1 year) × Legh. 91 ♂ (2 years)......	3	8
69.	„ 417 ♀ (1 year) × „ 369 ♂ (1 year)......	6	4

Table of Relationship of I.G. Birds which gave Mixtures.



In the above table all those that were tested and found to give no mixtures are labelled D, while those that gave mixtures are labelled DR. As stated in the text, 90 ♀ × 12 ♂, though supposed thoroughbreds, gave a mixture of 6 s.c. and 6 p.c. when bred together. The labelling D and DR is put in to show how far what is called hereafter (p. 117) the "First Hypothesis" agrees with the facts.

On the contrary, it must be noticed that all the nine "out-bred" birds gave mixtures as expected on the "Second Hypothesis" (p. 119).

White Dorkings and Leghorns giving Mixed Offspring in First Crosses.

As stated in Experiments 24—29 (p. 102) the three birds from the Cresswell strain showed practically complete dominance of the rose comb (59 r.c., 1 s.c.). As regards foot, all these six matings showed the extra toe dominant except one (Experiment 25), in which two chicks had no extra toe and four had an extra toe on one side only.*

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* As mentioned (p. 98), the mother of these chicks, Cr. 121 ♀, showed a secondary tinged with buff on the second moult, and it is not doubtful that the White Dorking is remotely connected with the coloured Dorking. This sign of impurity might be supposed to show impurity in comb, inasmuch as the Coloured or "Dark" Dorking is usually s.c., but its foot of course has the extra toes of the Dorkings.

Of the two birds, ♂ and ♀, from Miss Knowles, the cock only was tried with Leghorns. In each case he gave some recessives, both as regards comb and toe, as follows :—

70. Legh. Babr. 42 ♀ (2 years) × Dork. K. ♂ (1 year) gave in 1900—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
30	18	46	1	1

71. Legh. Babr. 42 ♀ (3 years) with Legh. Babr. 110 ♀ (3 years) } × Dork. K. ♂ (2 years) gave in 1901—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
31	21	64	1	2

72. Legh. Babr. 42 ♀ (3 years) alone × Dork. K. ♂ (2 years) gave in 1901—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
29	19	36	1	0

73. Legh. Babr. 110 ♀ (3 years) alone × Dork. K. ♂ (2 years) gave in 1901—

R.c.	S.c.	Both e.ts.
8	7	15

74. Brown Legh. Br. L. 1 ♀ (2 years) × Dork. K. ♂ (1 year) gave in 1900—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
35	36	59	7	5

75. Br. L. 1 and Br. L. 2 together (3 years) × Dork. K. ♂ (2 years) gave in 1901—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
57	68	93	17	16

Between these two hens the last results cannot be allotted with certainty, but it was known that Br. L. 1 ♀ contributed to these totals at the end of the season after removal of Br. L. 2 ♀.

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
25	28	46	3	5

25. In regard to *comb* this experiment has been given in the Mendelian group, for the r.c. showed full dominance so far as the numbers went. As regards foot-character the case belongs here.

Cr. ♀ 121 (2 years) × Brown Legh. ♂ (2 years) gave—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
22	0	16	4	2

It is to be remembered that the hen belonged to the strain of White Dorkings which, with other Leghorns, showed dominance of extra toe.

76. Legh. 378 ♀ (1 year) × Dork. K. ♂ (2 years) gave—

R.c.	S.c.	Both e.ts.
2	5	8

These birds were only together for a fortnight at the end of the season.

As told on p. 93, from Miss Knowles's two birds, which may or may not have been nearly related—were bred two pullets, Dorkings 262 ♀ and 263 ♀, and one cock, Dorking 258 ♂, which gave following results. Both pullets were exceedingly sterile. They were hatched on May 22 of the previous year, and so can hardly be considered very "late hatched."

77. Legh. 378 ♀ (1 year) × Dork. 258 ♂ (1 year) gave—

R.c.	S.c.	Both e.ts.	No e.t.
19	36	55	0

78. Dork. 262 ♀ (1 year) × Legh. 91 ♂ (2 years) gave—

R.c.	S.c.	Both e.ts.
1	1	2

79. Dork. 263 ♀ (1 year) × Legh. 373 ♂ (1 year) gave—

R.c.	S.c.	Both e.ts.
4	0	4

Matings with Members of Mixed First-cross Families.

A. *From Indian Game and Leghorns.*

Three first-cross pullets 111 ♀ and 151 ♀, both pea-comb birds, and 149 ♀, a single-comb bird, were bred with their own brother, 112 ♂ (all raised in Experiment 58), for the whole season 1901. These four birds were all white, ticked.

80. Cross-bred 111 ♀ p.c. (1 year) × cross-bred 112 ♂ p.c. (1 year) gave—

P.c.	S.c.	Lt.	Dk.
38	22	50	10

81. Cross-bred 151 ♀ p.c. (1 year) × cross-bred 112 ♂ p.c. (1 year) gave—

P.c.	S.c.	Lt.	Dk.
46	21	49	16

82. Cross-bred 149 ♀ s.c. (1 year) × cross-bred 112 ♂ p.c. (1 year) gave—

P.c.	S.c.	Lt.	Dk.
34	50	56	24

83. Three s.c. pullets, first crosses, cross-bred, ♀'s 44, 71, 117 (1 year), raised in Experiment 50, were bred for most of the season with a single comb cross-bred 97 ♂ (1 year) raised in Experiment 54. All four were white ticked birds. They gave—

P.c.	S.c.	Lt. down.	Dk. down.
0	149	106	40

These four birds with recessive combs therefore produced no dominant comb at all.

84. A pea comb cross-bred 77 ♀ (1 year) raised in Experiment 54 with the same cockerel as used in Experiment 83, for a few days only gave—

P.c.	S.c.	Lt. down.	Dk. down.
6	3	8	1

B. *From White Dorkings and Leghorns.*

85. Two r.c., e.t. pullets, cross-bred, 249 ♀ and 278 ♀, raised in Experiment 74 (out of Brown Leghorn 1 ♀ × Dorking K ♂), bred for the season 1901 with own r.c., e.t., brother gave—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.	Lt. down.	Dk. down.
131	53	135	8	49	131	44

86. A pullet, s.c., e.t., cross-bred, 317 ♀, raised in Experiment 70, was bred till end of May, 1901, with cockerel s.c., *no* e.t., cross-bred, 305 , raised in Experiment 74, gave—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.	Lt. down.	Dk. down.
0	60	45	1	14	60	0

In this experiment again, the birds with recessive combs have been unable to produce any dominant comb. On the other hand, the fact that the cockerel was without extra toes does not seem to have had any effect on the proportion of e.t. to no e.t., which are approximately 3 : 1, as would have been expected if the parents had been dominant first crosses from a Mendelian family. These birds had only one coloured grandparent, and are therefore unable to produce any dark-coloured offspring, in conformity to the expectation.

87. A pullet, own sister to those used in Experiment 86 (raised in Experiment 70), but *rose* combed, with extra toes, by the same ♂ 305, s.c., *no* e.t., gave—

R.c.	S.c.	Both e.ts.	No e.t.	Lt. down.	Dk. down.
8	7	10	5	15	0

88. The same cockerel, cross-bred 305 ♂, used in Experiments 86 and 87, was put for the latter weeks of the season 1901 with six

pure Leghorn hens of various ages and breeding. They collectively gave—

R.c.	S.c.	Both e.ts.	1 e.t.	No e.t.
0	152	77	1	78

138 are recorded as light chicks, and there were none dark.

Here again the cockerel, *without extra toes*, gives the same result as if he had been a Mendelian dominant first cross! The absence of dark-coloured chicks is, of course, to be expected, as only one grandparent was coloured.

Discussion of Non-Mendelian Group.

It has been seen that in the crosses both of Indian Game with Leghorns, and of Dorkings with Leghorns, the results divide themselves into two groups. In the first group the first crosses, almost without exception, exhibit the dominant characters, and the subsequent progeny produced by breeding these first crosses *inter se* obey Mendel's Law fairly well. There are departures from the law which may possibly indicate special disturbing causes, but the general applicability of the principle is unmistakable.

The second or non-Mendelian group of cases is much more obscure, and their significance is quite different as they are regarded in one of two ways. The question on which the whole difficulty turns may be then expressed: Can birds, which themselves exhibit dominant characters, even on crossing with recessive birds, produce recessive offspring *if they would not have produced recessive offspring when bred* inter se*?* Otherwise, though less correctly, the question may be expressed thus: Is the fact that certain supposed pure dominants gave some recessives when crossed with recessives, to be ascribed solely to the fact that the dominants were impure? "Pure" and "impure" are not here used quite in the ordinary sense of the fancier. "Pure" means producing gametes which all transmit the same character and are homogeneous; "impure" means producing gametes of more than one kind, heterogeneous in regard to the characters they bear. Simple purity of descent is not in question,* for as we now know, the "purity" required may be the attribute of any individual of the form DD or RR, though of immediately mixed descent. In Mendelian terms, does DR ever appear recessive in these cases, or does such a recessive appearance always indicate that the individual is really RR? Unfortunately the material

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* Inquiry as to whether recessives had ever occurred in the yards from which the birds in question came elicited that in the case of I.G. Brom. ♂ the question could not be answered. In the case of the Dorking, Miss Knowles very kindly writes that an occasional single comb is seen from time to time, perhaps about 1 in 30, and also an occasional four-toed bird; but that the number of such recessives is much greater when fresh blood is introduced.

for finally answering this question in the case of the *combs* is not before us. It was not until the bearing of the Mendelian discovery was fully realised, and its applicability to these phenomena shown, that the absolute necessity for a decision on this point became evident. Moreover, until at the very least three successive generations have been bred the point cannot be quite decided. We may then usefully at this stage consider the facts briefly in the light of each of these two hypotheses, and point out how far either of these suppositions is consistent with observation.

First Hypothesis: that every Recessive is, in composition, RR.

According to this view the two original Brom. birds must be regarded as of different composition, the ♀ giving × Leghorn LK ♂ (Experiment 20), 18 p.c. and 0 s.c. is probably to be considered as pure dominant, DD. The ♂, however, gave by three different Leghorn hens in

	P.c.	S.c.
Experiment 43........	7	18
" 44........	10	10
" 45........	7	5

He would therefore be regarded as a dominant cross, DR. We note that in Experiment 43 the numbers 7 : 18 are far from the expected 1 : 1, being 1 : 2·5. To this point reference will again be made.

The same ♂, whose possible "impurity" was then unsuspected, bred (see table, p. 112) with I.G. BSR ♀ of undoubted "purity," gave five birds, of course all p.c. We expect, then, that of these half were DD and half DR. But *all* these five I.G.'s, when crossed with Leghorns, gave mixtures, as told in Experiments 45—58, the proportion of p.c. to s.c. being again very various, though, as a matter of fact, the totals, 122 p.c., 113 s.c., approach the expected equality. Five is a small number for such a test, still it is noticeable that *none* of them appeared to be DD, while on this hypothesis *half* should have been so.

Of these five birds two were bred together, and, as told on p. 112, there was at once a mixture of peas and singles, 6 p.c., 6 s.c., the hypothesis expecting 3 p.c. : 1 s.c. Of these birds, unfortunately, two only, both p.cs., survived to be tested. *Both were pure dominants DD*, though DD : DR should here be 1 : 2.

One of the five birds (I.G. ♀ 17) here assumed to be DR. with three Leghorn ♂'s gave 48 p.c. and 41 s.c. (Experiments 49—51) closely approaching the expected equality.

This hen was bred with I.G. Rd. ♂. As to the latter the evidence is that he gave (Experiment 21) with a Leghorn ♀ 29 p.c. and 1 s.c., which is a close approximation to purity. With I. G. ♀ 17 he gave a family, all p.cs., of which one alone was tested, I. G. ♀ 37, proving (Experiment 63) to be, on the hypothesis, DR, and giving × Leghorns

373 ♂, 28 p.c. 29 s.c., or the expected 1 : 1. The same hen × I. G. 30 ♂, of established purity (Experiments 5—8), gave a family of Indian Games, all p.c. of course. Three of these were tested (Experiments 64—69), giving in each case a mixture, the proportions again varying.

In addition, therefore, to the five birds reared out of BSR ♀ × Brom. ♀, we have one bird out of I.G. 17 ♀ × Rd. ♂, and three birds out of I.G. 37 ♀ × I.G. 30 ♂, nine birds in all, which gave mixtures on crossing with Leghorns, and *none* which did not give mixtures, though the hypothesis expects that *half* of them would give such mixtures, and that *half* would not. This discrepancy, though far from amounting to proof, nevertheless gives a decided suggestion that the hypothesis we are considering is insufficient to thoroughly explain the phenomena. It must be noticed, too, that all the nine supposed DR birds were *out-bred*.

Taking now the Dorking cases, it is clear that as regards comb the Cresswell strain comes very near "purity," giving, on crossing with Leghorns (Experiments 24—29), 123 r.c., 1 s.c., 1 intermediate.

As regards extra toe, we have already called attention to the fact that as Experiment 25 shows, the evidence is not quite so absolute.

The Knowles strain was represented by two birds, K ♂ and K ♀. The male gave, on crossing with Leghorns, mixtures both as regards comb and toe (Experiments 70—76). The female, now dead, was never tested by crossing.

As the offspring of these two there are three birds of which two gave mixtures of combs on crossing (Experiments 77—79), and the third was insufficiently tested. So far, however, there is no mixture in regard to foot.

Finally, we have to consider the unexpected facts shown by Experiments 83, 86, and 88, in which it appeared that cross-bred birds (both Dorking—Leghorns and Indian Game—Leghorns alike) with recessive combs, whether bred together or with pure recessives, gave *only recessives* so far without exception. (Also in Experiment 82 a recessive crossbred with a dominant own brother gave a considerable excess of recessives, viz., 34 p.c. and 50 s.c.)

Now if the hypothesis we are considering be the true one, this fact becomes explicable; for in the cases where a mixture occurs on the first cross, we should thus expect that any recessive produced would be pure. This fact is so remarkable and so difficult of explanation on any other supposition that it may naturally be thought to outweigh all other discrepancies.

But this simple explanation is not applicable to the case of extra toe. There is so far the evidence of only one bird—the cross-bred 305 ♂. This bird, which had single comb and *no trace whatever of* *extra toe*, nevertheless when bred with pure Leghorn hens gave as many chicks with extra toes as without them (Experiment 88). As regards foot, therefore, this cross-bred recessive was not only not pure, but behaved exactly like a cross-bred dominant. Such a fact must be a complete refutation of the hypothesis of "impurity" as a sufficient explanation of the occurrence of recessive foot in the first crosses.

It also suggests very strongly that in cases where neither character has complete dominance, the first cross may produce equal numbers of gametes transmitting each character, just as in strictly Mendelian cases, a point on which more evidence is greatly needed. In such a case selection among the first crosses may effect nothing.

Second Hypothesis:. *that Recessives produced on the First Cross may be of the Composition DR, the usually dominant Character having Receded.*

That this hypothesis is a true one in the case of the extra toe is certain, as stated in the last paragraph. If, then, a character, usually recessive, may thus dominate in the first cross, it may become necessary to regard as crosses some of the recessives produced by cross-bred dominants bred *inter se*, and very serious complexity may thus attend the unravelling of breeding results, though the transmission of character may occur in the strictly Mendelian method by pure gametes.

Seeing that this may certainly be so in the case of feet, we have to consider how the facts stand in regard to comb.

A preliminary consideration which goes against the view that both the Brom. and K. birds were merely impure, in the ordinary sense of being sensibly mongrelised with some other breed, is the fact that none of the birds bred thus far show any unexpected character except in regard to comb. In other characters, notably the brown colour, a character especially complex and likely to show such impurity—there is no noticeable departure from the respective breeds.*

On the hypothesis now before us the question arises, Why is it that some birds should have given mixtures on crossing while others did not? Also, Why do some birds on crossing give mixtures in such different proportions? Until the facts were examined in the light of Mendel's discovery, it was proposed to answer these questions by reference to the suggested effect of *in-breeding*. The B.S. strain had been long in-bred, and the fact that on crossing they gave no mixture was attributed to this cause. On *out-breeding* this strain with Brom. ♂ (see table, p. 112), birds were produced which gave *mixtures* on crossing. On breeding two of these out-bred birds together, brother and sister, two birds, I.G. ♂ 59 and ♀ 120, were produced which were *wholly dominant*, again, as was supposed on account of the close breeding.

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* Beyond the occasional appearance of white feathers in the wing quills.

On again out-breeding the out-breds with I.G. Rd. ♂, the hen I.G. ♀ 37 was produced, which again gave mixtures. This hen by the in-bred ♂ 30, a pure dominant, gave again three birds, 416 ♀, 417 ♀, and 419 ♂, which all produced mixtures on crossing. This last fact was attributed to the circumstance that the mother, I.G. ♀ 37, was thoroughly out-bred. Thus *all* nine birds which gave mixtures, lettered DR in table (p. 112), were out-bred.

Again the Cresswell strain of Dorkings, which was stated to be closely bred, was found to show pronounced dominance. The Knowles strain on the contrary was almost certainly not much in-bred, and the only bird tested was found to give a mixture on crossing.

This is again noticeable in the experiments made with the Dorking ♂ K. Bred with two in-bred Brown Leghorn hens through two seasons (Experiments 74 and 75) the singles were in a slight excess, the numbers being in all 92 r.c., 104 s.c., while the same cock with two White Leghorns, not in-bred, gave 98 r.c., 65 s.c., or roughly 3 : 2, the excess being on the r.c. side (Experiments 70—73).

As regards foot, the evidence points in the same direction, the White Leghorns scarcely producing any birds without extra toes, though the in-bred Brown Leghorns produced about 10 per cent. Evidence of the same kind was seen in Experiment 25 when the male Brown Leghorn was used.

Thus after the first three years, when it had been found that the males, Leghorns 40 ♂ and 91 ♂ (Experiments 52, 54, and 56), gave a distinct excess of singles over pea combs, and that the in-bred Brown Leghorn 1 ♀ gave a greater proportion of rose combs than out-bred hens did with the same cock, the evidence taken with the obvious dominance of the in-bred B.S. Indian Games and the Cresswell Dorkings seemed to show that in-breeding had the suggested effect.

Reference, however, to the preserved dead chicks out of LK ♀ × I.G. Brom. ♂ (Experiment 43) previously misunderstood* showed that the numbers were as stated, seven pea comb and eighteen single comb. The mother, therefore, of 91 ♂, though herself not in-bred, gave an even greater excess of singles than 91 ♂, which was certainly *somewhat* in-bred.

It must also not be forgotten that even the most decided dominants did as a rare exception give an occasional recessive on crossing with pure recessive (see Experiments 13, 21, 22, 22*a*), so that the possibility is established that in birds which are unquestionably DR by breeding, the recessive comb *may* appear.†

To sum up: for the considerations already given, there is no *certain*

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* This cross was one of the first made, before the characters of the young chicks were properly appreciated.

† Unfortunately no such recessive was bred from, and it is therefore uncertain whether they would have proved pure recessives or not.

evidence that in-breeding has increased the dominance even on the dominant side, as the cases that at first sight point so clearly in that direction may, perhaps, be capable of another explanation.

On the recessive side the evidence is even more uncertain. It became early apparent that in the case of pure *recessives*, in-breeding did not have that strong influence on the determination of dominance which it may be suggested it had in the case of pure dominants; or rather, if this effect were produced, it was much less marked. As, however, none of the actual relationships between the original White Leghorns were known, it was not at all certain that, when birds of the same strain were mated together, the offspring would be very closely bred even for one generation. Lastly, the only recessive birds yet tried, which are known to be the offspring of brothers and sisters, have not yet shown any certain increase of dominance (Experiments 51, 63, and 66).

Whether or no any of the "prepotency"* yet observed can be ascribed to in-breeding, a question which must still be left open, there is the certain fact that very distinct "prepotency" did appear on the recessive side in many instances (Experiments 43, 50, 54, 56, 62, 68, also in 74, 75, and 77, as compared with 70—73). In two of these cases also there is evidence that the proportions in successive seasons were quite different (*cf.* Experiment 54 with 55, Experiment 56 with 57), but in some others the proportions remained almost identical in successive seasons (*cf.* 70 with 71, 74 with 75). In the former case it should be noticed that in Experiments 55 and 57 the I.G. hens were old, probably in their last season of laying, and though the hens in 75 and 71 were of the same age, yet 3 years of breeding does not in the case of Leghorns nearly finish the period of fertility, and in fact such decline had not begun.

In this connection reference should be made to the interesting result obtained by Ewart† in crossing a pure Turbit with a Jacobin-Barb cross-bred female. Though not on a statistical basis, the facts arrived at distinctly support the view that with the age of the mother, the nature of her gametes changed. It is not, however, certain that this change was merely one of dominance,‡ which is the interpretation Ewart suggests. For in the light of what we now know the *cross-bred* mother must herself have been producing various gametes transmitting various characters, and the difference in the results at different ages may consequently have been due not to a change in dominance, but to the production of gametes carrying different allelomorphs (see p. 138).

A question which has been constantly kept in view is the possibility that in mixed families some proportions may be more common than

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* This word is used as signifying determination of dominance.

† 'Sci. Trans. Roy. Dub. Soc.,' 1901, vol. 7, p. 360.

‡ Supplying the Mendelian term.

others. On the hypothesis that all such mixtures point to impurity on the dominant side, it is to be expected that the average of all such cases would show the proportions equal. This expectation as regards both kinds of dominant comb compared with recessive comb is very closely realised, the totals being 459 dominant, 475 recessive. This equality may, nevertheless, have been brought about by many causes, choice of pairs, &c., and cannot be regarded as significant. The attention of those who are practically engaged in such experiments may be called to the considerable frequency of cases where equality is approached, to several cases of 3D : 2R and to several cases of 1D : 2R. The observations are yet far too few to justify any weight being laid on these occurrences, which so far seem fortuitous.

Results of Breeding from Members of Mixed-first-cross Families.—On the "first hypothesis," assuming Mendel's law to be strictly followed, the results on using recessive members of mixed-first-cross families should be the same as when pure recessives were used. The only foot recessive yet tried did not give this result and therefore is plainly *not* RR as regards foot. The comb recessives, however, when bred together or with pure single-combed birds, did appear pure and incapable of transmitting the dominant character. On the second hypothesis this is the fact most difficult of explanation and is indeed entirely paradoxical.

Subsequent experiment alone can show whether the dominant comb may not again be produced; but for the present there is every indication of purity. We need not point out that the significance of such a fact in any consideration of the physiology of heredity must be very great.

Such cases, though seldom thoroughly investigated as yet, are, nevertheless, known to occur. In our own experiments one such example was seen in the stock, when there could be no question that when on crossing pure hoary and glabrous varieties, the latter (recessive) character appeared in the cross, such plants in subsequent breeding were found to be pure recessives. The famous *faux hybrides* of Millardet* are the best known illustrations of the same phenomenon.

Similarly on the first hypothesis all dominant cross-breds are to be DR, and the result of breeding from them should be the same whether they were members of mixed, or of purely dominant families, and we are to expect 3D : 1R when they are bred *inter se*. But if the second hypothesis is the true one, Mendel's law is no longer a guide, and we have no definite expectation. So far, we have only five experiments to judge from as to this point (Experiments 80—82, 85, and 87). The birds used in Experiments 80—82 were from Experiment 58, which was continued for a very short time only, giving 5 p.c. and 3 s.c. From this mixed family two pea-comb ♀ cross-breds × the same ♂ pea-

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* 'Mém. Soc. Sci. Bordeaux,' ser. iv, T. 4, p. 347.

comb cross-bred gave respectively 38 p.c., 22 s.c., and 46 p.c., and 21 s.c., or together 84 p.c. to 43 s.c., thus approaching 2D : 1R. But a single-comb cross-bred ♀ from the same family mated with the same male (Experiment 82) gave 34 p.c., and 50 s.c. She, however, must be supposed (p. 115) to be a pure RR, and thus we should expect equality in her offspring. Therefore we perceive that the cock was at this time almost certainly producing an excess of recessive germs ; and as the three hens used in 80—82 were all with him at the same time, it may well be this excess of recessives which has caused the numbers in 76 and 77 to depart from 3 : 1.

On the Dorking side in Experiment 85 two dominant first cross hens from Experiment 74 were bred with own dominant brother, giving 131 rose combs to 53 single combs, or 2·47 : 1. Again the recessives are in excess, and the only other evidence as to the cock is the slight indication given by Experiment 87, where there was the expected approximate equality in a total of only 15. Taken together the four comparable totals amount to 215 D : 96 R, or 2·25 : 1. Though the departure from 3 : 1 is here decided, it cannot yet be taken as conclusive against the view that we are here dealing with DR birds, for, as has already been seen, considerable fluctuations are to be expected.

Summary of Conclusions from Experiments with Poultry.

1. When distinct breeds are crossed together certain structural characters in particular strains may exhibit the phenomenon of dominance, the antagonistic character being recessive.

Dominant characters are pea comb, rose comb, extra toe, while single comb and the normal foot are recessive. In the case of each of these pairs of characters, the cross-bred may show some blending, and as regards pea comb crossed with single, or extra toe with the normal foot, the intensity of the dominant character is often considerably reduced. In these cases, it would be possible to recognise the cross-breds *as a rule* from the dominant parents, though sometimes the dominance may be complete. The recessive form is always quite distinct.

2. When the offspring of such crosses are bred together their progeny are mixed, some presenting the dominant, others the recessive character, in proportions following Mendel's law with fair consistency, though in certain cases disturbing factors are to be suspected.

3. When some strains possessing the usually dominant character were crossed with pure recessives, this first cross resulted in a mixture of dominants and recessives. Whether in the case of comb-characters such a mixture may be taken as proving that the dominant parent was itself giving off recessive gametes, or as indicating that the usually recessive character may sometimes dominate, there is not yet sufficient

evidence to show, for some of the facts favour the first hypothesis, while others point to the second.

That the recessive foot-character may sometimes dominate was established.

4. In favour of the first hypothesis (or perhaps that of "false hybridism") is the otherwise extraordinary fact that first-cross birds with recessive combs have so far proved to be pure in that respect and incapable of transmitting the dominant comb when bred either with other similar cross-bred recessives or with pure recessives (see p. 45).

5. The relative numbers of dominants and recessives in mixed first-cross families varied greatly, but whether the degree of consanguinity in the mating by which either parent had been produced was influential in affecting these proportions was not certainly determined, though perhaps the balance of evidence is in favour of a positive influence.

6. In White Leghorns, white plumage is dominant over brown plumage, and the offspring of the first crosses bred *inter se* consisted of light and dark birds in the proportions of 3 : 1, judging by the down of the young chicks.

The dark class thus produced consists of various types, of which some are definite. A few individuals approach the dark grandparental form, while many depart widely from it, indicating that the original dark coloration is probably a compound character, capable of being broken up into component characters. The gametes, therefore, which transmit the recessive dark colours are, after crossing, of several kinds, the number of such kinds being unknown. The dark forms may be supposed to result from the union of two dark-bearing gametes, while the light birds may be supposed to result from the union either of two dominant white-bearing gametes, or of one of them with a dark-bearing gamete. Consequently the dominants (as regards plumage) resulting from the first crosses bred together are also of several types.

7. White shanks and bill are almost wholly dominant over yellow shanks and bill. The first crosses bred together give the expected mixture of whites and yellows, though in what proportions has not yet been determined.

8. There is no correlation yet perceived between the characters of comb, foot, and colour of plumage. Possibly the colour of shanks and bill has some correlation with that of plumage.

9. One definite case of distinction between the results of reciprocal matings was found (see p. 95).

[Note, added March, 1902.

So far no exception to the purity of the extracted recessive combs has occurred, but no opportunity of fully testing the purity of the recessive foot-character has yet occurred.]

PART III.—THE FACTS OF HEREDITY IN THE LIGHT OF MENDEL'S DISCOVERY.

As was stated in the introduction to this paper, with the discovery of the Mendelian principle the problem of evolution passes into a new phase. It is scarcely possible to overrate the importance of this discovery. Every conception of biology which involves a knowledge of the physiology of reproduction must feel the influence of the new facts, and, in their light, previous ideas of heredity and variation, the nature of specific differences, and all that depends on those ideas must be reconsidered, and in great measure modified.

If we turn to any former description of breeding experiments we generally perceive at once that the whole account must be re-stated in terms of Mendel's hypothesis, and that the discussions and arguments based on former hypotheses are now meaningless. As an illustration we may take the account which Darwin gives of his experiments with peloric Antirrhinum.* He crossed the peloric form with the normal and *vice versâ*. The first crosses were all indistinguishable from the normal or zygomorphic form. These were allowed to fertilise themselves, and gave a crop consisting of 88 normals, 2 intermediates, and 37 perfectly peloric. He discusses these results on the hypothesis that the normal plant has a "tendency" to become peloric, and the peloric a "tendency" to become normal, "so that we have two opposed latent tendencies in the same plants. Now with the crossed Antirrhinums the tendency to produce normal or irregular flowers, like those of the common Snapdragon, prevailed in the first generation; whilst the tendency to pelorism, appearing to gain strength by the intermission of a generation, prevailed to a large extent in the second set of seedlings. How it is possible for a character to gain strength by the intermission of a generation will be considered in the chapter on pangenesis."

Now, of course, we can perceive that the zygomorphic form is dominant and the peloric recessive, and that the arguments based on other hypotheses have no longer any significance. It would be a useful task to go similarly through the literature of breeding and translate the results into Mendelian terms. Such an exercise would show that the change which must now come over the conceptions of biology can only be compared with that which in the study of physical science followed the revelations of modern chemistry.

The outcome of such a revision of current conceptions it is impossible to foresee, but we propose in the present paper to consider some of the more important questions which are immediately raised.

To denote the new conceptions some new terms are needed. Several have already been suggested by Correns, but in practice we have not found his terminology altogether convenient, or that it meets the new

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* 'Animals and Plants,' vol. 2, p. 46, ed. 1885.

requirements. Correns proposes the terms "heterodynamous" and "homodynamous" to express that an organism is dominant or not dominant in respect of a given character. There are unfortunately objections to the use of these terms, though in some respects they are very suitable. First, they are in use by Weismann and his followers in quite different senses, as Correns states. Secondly, it is not clear whether they are to be applied to the variety, the individual, or the character. Besides these objections, it is fairly clear that dominance is a phenomenon presenting various degrees of intensity; and while the single phenomenon of dominance is well expressed by that word itself, other conditions probably consist of various phenomena which are not conveniently denoted by one word.

Correns' terms "homöogonous" and "schizogonous" cannot as yet be used with precision to mean more than breeding "true" and not breeding "true," and, for reasons given later, the metaphor of splitting may be incorrect.

The terms also "*halb-identisch*" and "*conjugirte*" as applied to characters, are already fairly well expressed by the words in perfect or in imperfect correlation, which are already well understood. It would be confusing to introduce the metaphor of conjugation to denote these ideas.

But while doubting whether this terminology already suggested will be found adequate, we do not propose at present to substitute new terms for the same phenomena. In our view, there are other conceptions arising from the Mendelian discoveries for which brief expressions are absolutely required, and for these we suggest the following terminology.

In the introduction (p. 6) we attempted to distinguish precisely the essential fact discovered by Mendel, and to separate it from other subordinate appearances. We may now briefly recall and amplify that reasoning, showing how we propose to denote the several phenomena.

By crossing two forms exhibiting antagonistic characters, cross-breds were produced. The generative cells of these cross-breds were shown to be of two kinds, each being pure in respect of *one* of the parental characters. This purity of the germ-cells, and their inability to transmit both of the antagonistic characters, is the central fact proved by Mendel's work. We thus reach the conception of unit-characters existing in antagonistic pairs. Such characters we propose to call *allelomorphs*,* and the zygote formed by the union of a pair of opposite allelomorphic gametes, we shall call a *heterozygote*. Similarly, the zygote formed by the union of gametes having similar allelomorphs, may be spoken of as a *homozygote*. Upon a wide survey, we now recognise that this first principle has an extensive application in

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* Correns speaks of the two opposite allelomorphs as a "*Paarling*."

nature. We cannot as yet determine the limits of its applicability, and it is possible that many characters may really be allelomorphic, which we now suppose to be "transmissible" in any degree or intensity. On the other hand, it is equally possible that characters found to be allelomorphic in some cases may prove to be non-allelomorphic in others.

It will be of great interest to determine how far the purity of the germ-cells in respect of allelomorphic characters is an absolute rule, or whether there are exceptional cases in which such purity may be impaired. That such exceptions may arise is indeed almost certain from the evidence of "mosaic" fruits in *Datura*, where it was shown (p. 23) that the otherwise pure extracted recessives (thornless) showed exceptionally a thorny patch or segment. Unless this is an original sport on the part of the individual, such a phenomenon may be taken as indicating that the germ-cells may also have been mosaic.*

Indeed all that we know of the occurrence and distribution of variation among repeated parts, would lead us to expect such a possibility with confidence.

This is a question we can analyse no further. Were it possible to do so, it might be a real help towards getting a picture of the actual process of heredity.

But besides the strictly allelomorphic or Mendelian distribution of characters among the gametes (with or without mosaics), we can imagine three other possible arrangements. (1) There may be a substantial discontinuity, the two types of gamete being connected by a certain proportion of intermediates, such as are often met with in cases even of almost complete discontinuity among zygotes. (2) There may be continuous variation among the gametes, shading from gametes pure to the one type, to gametes pure to the other type, the intermediates being the most frequent. (3) There may be no differentiation among the gametes in respect of parental characters at all, each representing the heterozygote characters unresolved. This last is the homoögonous type of Correns. By a sufficiently wide survey, illustrations of each of these systems and of intermediates between them, will doubtless be found, and the classification of gametic differentiation according to these several types, in respect of various characters, in various species, will be a first step towards the construction of a general scheme of heredity.

In gametic variation we thus meet in fact the same series of possibilities with which we have been familiar in the variation of zygotic organisms.

The second fact observed by Mendel is that each heterozygote produces on an average equal numbers of gametes bearing each allelo-

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* Conceivably the cases of poultry having one foot with extra toe and one normal, may be of a similar nature, though for various reasons this is unlikely.

morph of each pair. This is only enunciated as an *average* result. Unfortunately, the determinations of the results for individuals are still few, but from those that have been made, and even from the few recorded by Mendel himself (p. 13), we see that the fluctuations are so great, that we must suspect some special sources of disturbance. Contributing to the average result of 3 : 1 as between round and wrinkled peas, he mentions as extremes 43 : 2, 14 : 15; and between yellow and green 20 : 19 and 32 : 1. It is obvious that this suggests either that there has been for some cause selection among the germ-cells originally equal in numbers, or that the numbers were originally unequal, or that the assortment of male and female germs was not governed by pure chance. Probably a series of individual determinations when seriated would throw light on the nature of these remarkable fluctuations which have been observed in almost all the subjects studied. From what we already know (see p. 121), in respect of the output of the two kinds of gametes, it is fairly certain that fluctuations take place, corresponding probably with changes in health, age, and other conditions.

From analogy—an unsafe guide in these fields—and from what is known of discontinuous variation in general, we incline to the view that even though the figures point to a sharp discontinuity between dominant and recessive elements, we shall ultimately recognise that the discontinuity between these elements need not be *universally* absolute. We may expect to find individuals, and perhaps breeds or strains, and even individual gonads or groups of gonads, in which the discontinuity is less sharp even in respect of these very characters; similarly, for such units definite departures from statistical equality between D and R germs may be expected. In *Pisum*, for instance, we cannot be far out in considering an average of 50 per cent. D and 50 per cent. R as a close approximation to the truth for both male and female cells, but there is nothing yet which proves even here that the discontinuity *must be always and absolutely complete.*

Similarly, we are not compelled to accept the proposition that germ-cells of each allelomorph *always* exist on an average in equal numbers. The proofs of the two propositions are unfortunately as yet interdependent. The purity of the extracted recessives and dominants has been tested, and we can in such cases accept it as a fact: the *universal* purity of the gametes we cannot test. For, any dominant which gives rise to a recessive offspring, we should class as a cross-bred, because cross-breds are like dominants in appearance. Similarly, any partially impure recessive would be classed as a cross-bred. If the number of germs of each kind borne by the cross-bred is sensibly unequal, or the discontinuity between them sensibly lessened, we can perceive a result, but we shall not know to which cause to ascribe it. The statistical method unfortunately cannot distinguish between the two causes in such a case. Readers of Mendel's paper will be aware that he laid down no universal rule as to the absolute purity of gametes, but merely pointed out that his results were explicable on the hypothesis of such purity.

The statistics, however, are not so precise as to compel us to accept *both* that the germs of the cross-breds are *always* pure, and that they are *always* produced on an average in equal numbers.

The next point arising immediately out of Mendel's work concerns the characters of the heterozygote. In the *Pisum* cases the heterozygote normally exhibits only one of the allelomorphs clearly, which is therefore called the dominant. It is, however, clear from what we know of cross-breeding, that such exclusive exhibition of one allelomorph in its totality is by no means a universal phenomenon. Even in the pea it is not the case that the heterozygote always shows the dominant allelomorph as clearly and in the same intensity as the pure dominant, and speaking generally, heterozygotes, though in numerous instances readily referable to one or other of the allelomorphic types, exhibit those types in a more or less modified form.

Besides these, there are undoubtedly cases in which the heterozygote may show *either* of the allelomorphs, though one is commonly dominant. In the poultry crosses it was shown that the usually recessive foot-character (want of extra toe) may appear in the cross-bred. The want of dominance of hoariness in *Matthiola* seen in exceptional cases is a wholly different phenomenon (see pp. 45 and 79).

From the analogy of poultry, it is scarcely doubtful that polydactylism in man is also allelomorphic to the normal, and here from the tables of heredity already recorded,* there is good evidence that both the normal and the polydactyle offspring of one polydactyle parent can transmit the polydactylism; in other words, the heterozygote may exhibit either allelomorph. Cases of the same phenomenon can indeed be multiplied. It must, however, be remembered that what is accepted as evidence of alternative inheritance, is not a proof that the dominance of either allelomorph is imperfect. This can only be known for certain when it has already been established that individuals showing either of the two allelomorphs can, when mated with an individual showing the same allelomorph, produce both allelomorphs among their offspring.†

This leads to a point of great importance to the evolutionist We

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* For examples see Fackenheim, 'Jen. Zt.,' xxii, p. 343.

† For the present, therefore, we are not entitled to assume that the numerous cases among Lepidoptera of varieties breeding together with a discontinuous mixed result are allelomorphic, probable as this conclusion is. Such cases are those of *Amphidasys betularia* and *doubledayaria; Aglia tau* and *lugens; Angerona prunaria* and *sordiata; Miana strigilis* and *æthiops*, &c. See Standfuss, 'Handb. d. pal. Gross-Schmetterl.,' 1896, p. 305, *et seq.*

have been in the habit of speaking of a variation as discontinuous, in proportion as between it and other forms of the species intermediates are comparatively scarce when all breed freely together. In all cases of allelomorphic characters we can now give a more precise meaning to this description. It must now be recognised that such a population consists, in respect of each pair of allelomorphs, of *three* kinds of individuals*, namely, homozygotes containing one allelomorph, homozygotes containing the other allelomorph, and heterozygotes compounded of both. The first two will thus always form discontinuous groups, and the degree to which the heterozygotes form a connecting group, will depend on whether one allelomorph regularly or chiefly dominates in the heterozygote, or the allelomorphic characters completely or partially blend in the heterozygote. *Such discontinuity will in fact primarily depend not on the blending or non-blending of the characters, as hitherto generally assumed, but on the permanent discontinuity or purity of the unfertilised germ-cells.*

It will be of great interest to study the statistics of such a population in nature. If the degree of dominance can be experimentally determined, or the heterozygote recognised, and we can suppose that all forms mate together with equal freedom and fertility, and that there is no natural selection in respect of the allelomorphs, it should be possible to predict the proportions of the several components of the population with some accuracy. Conversely, departures from the calculated result would then throw no little light on the influence of disturbing factors, selection, and the like.

From the circumstance that dominance of either character is no essential accompaniment of allelomorphism, it must be determined whether the proportions of the two kinds of gametes produced by the heterozygote will vary with its individual character. Bearing on this question the experiments are very few. The determination from statistical study of zygotes must be exceedingly difficult, seeing that *both* resulting forms may be heterozygous. The ratio in which the heterozygotes are distributed in the second generation need not be the same as it was in the first, and unless this can be determined it will be almost impossible to get further with this particular inquiry.

Another difficulty will be found in the possibility that when the first cross-bred generation gives a mixture, the forms showing the usually recessive character (both in this and subsequent generations) may be *pure* recessives as regards their own gametes also (false hybrids of Millardet, see p. 154) though heterozygous in origin. To solve these difficulties before the gametes can be microscopically differentiated may be still impossible.

We have now simple and convincing explanations of many facts hitherto paradoxical.

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* Four, if reciprocal heterozygotes are not identical.

1. *Heterozygous Forms.*—It has long been known to breeders that certain forms cannot be fixed by selection indefinitely continued. In other words, when the most perfect examples of such forms are bred together, though they produce some offspring like themselves, they have also a large number which do not resemble them.

A case of this kind is seen in breeding crested canaries. The kind of crest desired for exhibition can, according to canary-fanciers, be produced most easily by mating crested birds with non-crested, or plain-heads as they are called. If it be supposed that the crested character is usually dominant, we have a simple explanation. When crested birds are bred together a number of birds are produced whose crests are coarse and stand up and others without crests. The latter are the recessives; the former we may suppose to be the pure dominants. What the fancier wants is a crest composed of long feathers lying evenly down over the head. These may be the heterozygotes, and consequently cannot breed true or be fixed by selection. Such birds bred together, give many plain-heads and birds with coarse crests. Fanciers hold that the plain-heads needed for crest-breeding should be themselves crest-bred, *i.e.*, from families which have had crests among them. On the view here suggested this is probably a superstition, though one can easily see how it may have arisen.

If two crested birds are bred together it is advised that they should have imperfect crests, in all probability another form of the heterozygote.*

Another case, to which our attention was called by Mr. G. Thorne, of Broxbourne, is that of the Golden Duckwing Game Fowl. This colour can be produced by crossing Black-Reds with Silver Duckwing; but on attempting to breed the Golden Duckwing true, the colour breaks up again into its components.†

Probably the impossibility of fixing certain colours in Pigeons also illustrates the same phenomenon.

Such forms have hitherto been regarded as exhibiting "instability." Of this instability there is now a satisfactory account.

A more complex instance of this may be the Andalusian fowl. The colour is a blue-grey mixed with dull black. The breed will not continue true to colour. Though a considerable proportion of Andalusians are produced, a number will be hatched which are too dark or too light in various ways and proportions. Selecting the best Andalusians effects nothing, and the constancy does not increase. There is, therefore, a strong probability that the Andalusian is a heterozygote,

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* An account of these facts is given in Blakiston, Swaysland, and Wiener's 'Canaries and Cage Birds,' p. 128. When birds with good crests are bred together the recessive "plain-head" is often produced, a fact which has been exaggerated by various writers into the statement that the offspring of cresteds are *always* plain-heads, or even always *bald*.

† See also Lewis Wright, 'Book of Poultry,' 1886, pp. 289 and 356.

though, doubtless, of a complex nature (*cf.* p. 144). Its gametes do not fully correspond to it, and its colour must be produced by a combination of dissimilar allelomorphs.

A point of great practical and theoretical importance would be the determination whether the increased vigour so commonly observed in the offspring of some crosses is or is not correlated with the union of dissimilar allelomorphs. Hitherto we have spoken of all the offspring of crossing as "crosses," alike. We must now recognise that when heterozygotes are bred together their offspring *may not be crosses at all.* The great vigour seen in the first cross is known not rarely to decline in the next generation bred from them, and it may be possible to see whether such vigour was in reality associated with the union of any recognisably dissimilar allelomorphs.

The existence of forms which are exclusively heterozygous leads to the contemplation of another possibility. In the heterozygotes we have spoken of, both sexes of course bear gametes transmitting each allelomorph. If, however, one allelomorph were alone produced by the male and the other by the female we should have a species consisting *only* of heterozygotes.

So long as the heterozygotes bred together, the offspring in such a case would come true, but a proof that they were heterozygotes would be obtained by crossing them with another species or variety. It would then be found that reciprocal crosses would not give the same result. That this is actually the case we know in certain instances, of which the most familiar amongst animals is perhaps that of the Mule (Mare × Jackass) and the Hinny (She-ass × Stallion),* and amongst plants the hybrids of *Digitalis.*† In most treatises on crossing other cases are referred to, and though probably many of them are based on experiments insufficiently repeated, there can be no doubt many are authentic. Gärtner‡ acutely observes that the phenomenon of dissimilarity between the results of reciprocal crosses is more likely to be found among diœcious forms.

2. *Selection and the Phenomenon of Dominance.*—We have seen that the want of fixity in certain forms, though continually selected, may at once be explained by the hypothesis that they are heterozygous only, and have no gametes corresponding to them. Another illustration of the failure of selection is the constant recurrence of a particular "rogue" in the best strains. Seed is never taken from such rogues. Every year they may be pulled up as soon as detected, but they continually reappear.

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* A good description of the differences between these forms is given by Cornevin, 'Traité de Zootechnie,' 1891, p. 641.

† See Focke, 'Pflanzenmischlinge,' 1881, p. 322; and Gärtner, 'Bastarderzeugung,' 1849, p. 225. Other examples are given by Gärtner, *ibid.*; and by Swingle and Webber, 'Year-book Dept. Agric.,' 1897, p. 401.

‡ *Loc. cit.*, p. 228.

The hypothesis that such a "rogue" is a recessive form *may* give a complete explanation of this phenomenon in many cases. Selection from *individuals* of known fertilisation would at once test the truth of this view, and might provide a means of producing a pure strain once and for all from the pure dominants.

It is well known that some of the best modern beardless wheats which have been raised of late years by crossing distinct varieties will give a small proportion of bearded plants. This is, of course, called "reversion" to a bearded ancestor used in the original cross.

From the experiments of Rimpau,* we find that when bearded and beardless varieties are crossed, beardlessness is dominant, and the bearded character is recessive. By subsequent breeding a form is produced with a desirable character, and after a few years of selection it is found to give this character with sufficient purity and it is put on the market. It may be a bearded or a beardless form, but if the latter, the chances are that it will always produce a certain proportion of bearded plants.† This may happen in every case where there has been a *promiscuous* selection of many dominant plants, for any one of these may be a heterozygote and bear in each year both dominant and recessive germs.

The fact that the hornless breeds of goats still give some horned offspring is probably referable to the same cause. The point is of course not certain, but from the analogy of cattle (see p. 140) we may anticipate that the hornless form is dominant. In the polled breeds of cattle, which are never *promiscuously* selected, the polled character has naturally been easily fixed pure, but in goats selection among the *ewes* has been probably to a large extent promiscuous.

The phenomenon is without doubt occurring very widely in nature. To it we may perhaps attribute the undiminished persistence of some weakly varieties, which are unceasingly exterminated by natural or artificial selection without ever leaving offspring. Cases have only to be looked for to be found in abundance. We may note the paradox that, for anything we know to the contrary, a recessive allelomorph may even persist as a gamete *without the corresponding homozygote having ever reached maturity in the history of the species.*‡ It would be premature to trace out the deductions to which this suggestive fact points, but we see at once that it may give the true account of the phenomenon that

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* 'Landw. J. B.,' 20.

† Such a variety is Garton's Red King.

‡ [In illustration of such a phenomenon we may perhaps venture to refer to the extraordinarily interesting evidence lately collected by Garrod regarding the rare condition known as "Alkaptonuria." In such persons the substance, alkapton, forms a regular constituent of the urine, giving it a deep brown colour which becomes black on exposure. The condition is exceedingly rare, and, though met with in several members of the same families, has only once been known to be directly transmitted from parent to offspring. Recently, however, Garrod has

domesticated forms constantly give rise to varieties not met with in the wild state, a fact often ascribed on insufficient grounds to the action of changed conditions in producing greater *variability*.

It will be clear—a point which may have some economic importance—that in any such case the recessive "rogue" can be eliminated by selection from *individual* plants or animals, breeding only from those which give no recessives on being self-fertilised, if hermaphrodite. If the organism be diœcious the process will be more elaborate, for it will be first necessary to test for recessive allelomorphs by fertilising with a recessive, and afterwards to fertilise those that gave no recessive offspring, with a dominant similarly proved to be free from recessive influence. Nevertheless it is certain that by this process alone can a strain of pure dominants be readily made.

"Purity" then acquires a new and more precise meaning. An organism resulting from an original cross is not necessarily pure when it has been raised by selection from parents similar in appearance for an indefinite number of generations. *It is only pure when it is compounded of gametes bearing identical allelomorphs, and such purity may occur in any individual raised from cross-bred organisms.*

An organism can be strictly defined as genetically pure if all its gametes when united with similar gametes reproduce the parent identically; and in practice the only way in which such purity can, by one breeding, be tested, is by crossing the organism in question with pure recessives.

There are also other classes of cases where progressive selection fails not only to fix a particular variety but to diminish the proportion of "rogues" beyond a fairly definite limit. We may first consider how far the principle of dominance may give an acceptable account of such cases.

In his most valuable book, 'Die Mutationstheorie,' 1901, Professor de Vries devotes a chapter to the consideration of such phenomena, pointing out in a number of cases that progressive and continued selection has failed to fix a particular character. He draws the conclusion that such characters distinguish "half-races," as he calls them, which cannot be bred pure.

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noticed that no fewer than five families containing alkaptonuric members, more than a quarter of the recorded cases, are the offspring of unions of *first cousins*. In only *two* other families is the parentage known, one of these being the case in which the father was alkaptonuric. In the other case the parents were *not* related. Now there may be other accounts possible, but we note that the mating of first cousins gives exactly the conditions most likely to enable a rare and usually recessive character to show itself. If the bearer of such a gamete mate with individuals not bearing it, the character would hardly ever be seen; but first cousins will frequently be bearers of *similar* gametes, which may in such unions meet each other, and thus lead to the manifestation of the peculiar recessive characters in the zygote. See A. E. Garrod, 'Trans. Med. Chir. Soc.,' 1899, p. 367, and 'Lancet,' November 30, 1901.]

The cases taken are many-leaved clovers, a polypetalous Ranunculus, several plants with variegated foliage, and the biennial forms of certain species.

Selection in each case at first rapidly increases the proportions in which the selected form appears among the offspring, but soon a maximum effect is produced which is not surpassed.

Now in each of these examples fertilisation was left to insects, and though seed was saved from individual plants it is not in dispute that cross-fertilisation between them occurred. In Mendelian terms some might be pure D, some pure R, and some DR. Supposing dominance complete, eradication of the pure R forms annually does not extinguish them, for by the breeding of the DR forms *inter se* they will be continually reproduced.

There are no doubt many overlying complications in each of these cases, as, for instance, the probability that dominance is in these instances imperfect, but these will not change the main result.

The case of the biennial plants is especially interesting, as here we have strong indications that treatment and conditions may determine which character shall appear. For example, de Vries quotes the evidence of the Sugar Beet, a plant of great economic importance, to the breeding of which much attention has been devoted.

The plant which forms the large sugar-bearing axis is a biennial and does not flower until it has made the sugar-store. But from the best seed which has for generations been saved from such plants only, there arises a small percentage of an annual form which runs to seed without making a thick root at all. After years of selection the proportion of such rogues is not diminished. Now, if it could be supposed that the annual is recessive and the biennial dominant, this is partly explained. On selection, seeds are taken from dominants only. But some of these will be pure dominants and others will be heterozygotes bearing *both* allelomorphs. The latter will each year give rise to a certain number of pure recessives, compounded of two recessive gametes. In the first years of selection, the proportion of recessives will be diminished rapidly by choosing seed from dominants only, but further *promiscuous* selection of dominants, unless continued for an indefinite time, will not altogether remove the recessives, for they arise from the dominants themselves.*

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* It is of course only a conjecture that the biennial form is dominant in these cases, but, owing to the great importance of the subject, it seems worth while to call the attention of those interested to the possibility. Among the many investigations already made on the Beet it does not appear that the simple experiment has been tried of seeing if the annual or biennial form can be bred true from *individual* plants fertilised under proper precautions. Still less has the possibility of dominance been investigated. The only evidence known to us is that of Rimpau, that when the annual *Beta vulgaris* was grown near the cultivated form it bore two seeds which proved biennial and fifty-eight which were annuals. Rimpau

But in these forms it is well known that several kinds of treatment, exposure of the young plants to frost, over crowding, heavy manuring, and forcing, will greatly increase the proportion of "runners." In the case of *Œnothera* de Vries has made some very convincing experiments, clearly proving this fact, and Rimpau has done the same for the Beet, showing that the number of " runners " can thus be greatly increased. There are then some which are biennial in any case, some which are biennial or annual according to treatment, and some which are in any case annual. This is strongly suggestive of the three Mendelian classes.

De Vries has also experimented by selection from the annual plants, getting of course a higher proportion of annuals. But it must be remembered that in order to prove that the annual character is recessive, and that it can, as such, be fixed by one selection, it is necessary to ascertain first that the plant chosen is not what de Vries calls a "facultative" annual—on this hypothesis, a DR—and secondly that it has not been cross-fertilised, particulars not yet forthcoming.

But even if the hypothesis of dominance could be successfully applied to these cases, there are others at first sight similar, where it cannot be thus applied; for example, instances of varieties recessive in their differentiating character, producing annually a small but sensible number of a particular "sport," exhibiting a character already known to be dominant. Here we must suppose either that we meet the phenomenon of an *originating* variation—the "mutation" of de Vries: or possibly, which appears to be de Vries' view of half-races—the output of a certain number of such aberrant gametes is normally incidental to the development of the type-gametes. An objection to the latter deduction in some cases exists in the fact that the "sports" in question may be exceedingly rare, and therefore produced by few individuals only.*

3. *Skipping a generation.*—That marked individual peculiarities fail to appear in the immediate offspring, but may reappear in a subsequent generation has been often observed, and the fact has taken a great hold on the popular imagination. It has not yet been shown that the distribution of any of these characters among the different generations in any line of descent is other than is to be expected on the hypothesis of pure chance. Nevertheless we have now in the phenomenon of dominance a fact which may possibly be a real element

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conjectures that the two were crosses with the cultivated form, in which, as we should now say, the latter was dominant. But *B. patula*, an annual, emasculated and fertilised by cultivated Beets promiscuously, gave annuals only. Here there is a cross with another species, and the evidence is of doubtful application.

* Excellent illustrations of this phenomenon in the case of high-class Peas have been lately supplied to us by Mr. Arthur Sutton. Of these we hope to give details hereafter.

in the causation of such appearances, and those who are familiar with statistics of inheritance, in man for example, might usefully study them with the possibility in view. The absence of the character in the first generation may indicate merely that it is recessive, and its reappearance in the next generation may be due to the heterozygote having bred with another individual also bearing the recessive allelomorph.

4. "*New*" *characters may be dominant.*—We cannot as yet perceive any properties common to dominant as compared with recessive characters. It will be noted, however, that the view of many naturalists that the phylogenetically older character is prepotent, or, more correctly, dominant, is by no means of universal application. In poultry, for instance, both pea and rose combs are dominant against single, though the latter is almost certainly ancestral; the polydactyle foot is dominant against the normal, though a palpable sport. A point of some interest is that in both wheat and barley the beardless form is dominant, though we naturally, though perhaps incorrectly, regard it as a state normal in the one species, but an innovation in the other.

In cattle the polled form is dominant over the horned, though the former is a character which in our cattle has certainly arisen since domestication.

5. *Prepotency.*—The conception of dominance avoids certain difficulties which are involved in the use of the term "prepotent." As we now know that the allelomorphs of the several characters may be quite independent, it is confusing to speak of the prepotency of an individual when all that we know is that one or more of its characters is dominant over the contrary character. Of the dominance or prepotency of the *whole* we know nothing. The diversity of the views which have been at various times expressed as to the respective powers of mother or father to confer special qualities has probably arisen from confusions thus caused. If the term prepotency is to be preserved it must be applied to characters rather than to organisms, and its use must be restricted to cases in which the character so qualified has been actually tested by combination with the contrary allelomorph in one heterozygote.

We have been accustomed to consider that a variety may be sometimes prepotent in respect of a given character and sometimes not prepotent. The whole evidence on which this view is based will in many cases now require careful verification, for, as was fully discussed in the case of poultry, such a result may really be due to an unsuspected heterozygote having been sometimes used for the other parent. The evidence, for instance, that on crossing pea comb and single comb the offspring may be sometimes pea and sometimes single would formerly have been thought a clear proof that pea comb was not always dominant, whereas it is now certain that much fuller evidence is needed to establish this proposition.

The existence of the so-called "false" hybrids of Millardet (see p. 154) is an even more serious difficulty besetting the conception of prepotency, for here, though the cross-breds are produced by a union of the male and female gametes of two varieties, it is quite uncertain that the characters of both parents are introduced at all. (See p. 155.)

As a rule fair uniformity prevails among the results of first crossings, and in every case in which a mixture of forms occurs the question must now be asked *whether the fact is not a proof that either or both of the parents are actually producing more than one sort of gametes.* It is, no doubt, possible to conceive of the elements contributed by the two gametes respectively as engaged in a conflict so balanced that some supervening circumstances may give dominance to either side with varying frequency; but from what we now know of the nature of heredity, the conception of dissimilar gametes borne by one or both parents is just as easy to form, and no less probable on the facts.

6. *Sex.*—It is often profitable to compare the phenomena of variation with those of sex, and if the suggestion alluded to in the last paragraph be found true, it is worth reflecting whether the determination of sex may not sometimes be a phenomenon similarly conditioned.

[Note, added March, 1902.

There is already a considerable body of evidence in favour of the view that difference of sex is primarily a phenomenon of gametic differentiation. The evidence, however, seems to point to the conclusion that the differentiation is sometimes a phenomenon of the male cells and sometimes of the female cells, sometimes perhaps of both. Our attention has been called to a note by McClung,* suggesting that the differentiation of the spermatozoa of many insects and of some other Anthropods, according as they do or do not contain the "accessory chromosome," may be an indication of differentiation in regard to sex. This body has been the subject of extensive study on the part especially of the American cytological investigators, and further researches regarding it may be a most profitable field of inquiry.

The fact that in *Nematus ribesii*,† and in the Hive-bee, the unfertilised eggs produce males only, seems to prove that in those cases the female cells are carriers of the male character only, though whether there is sex-differentiation of the male cells is not yet known.

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* 'Anat. Anz.,' November, 1901, p. 220.

† Professor Miall has given me a reference to Cameron, 'Phytoph. Hymenop., Ray Soc. Monogr.,' vol. 1, p. 26, where authorities are quoted. He tells me that the same result was obtained in experiments of his own.

On the other hand, we have more frequent cases of unfertilised eggs in other types producing females only.

But from the observations of de Buzareingues,* it appeared that there is a more or less definite distribution of the sexes among the seeds of diœcious plants, the females being more commonly derived from seeds of one region, and the males from those of another. This of course is no proof of *original* differentiation of sex among the female cells, but it is readily consistent with that hypothesis.

On the other hand, as on the whole *against* the hypothesis that sex depends chiefly on gametic differentiation, may be mentioned observations—especially those of Wichura ('Bastardbefruchtung,' p. 44)—that the statistical distribution of sex among first crosses shows great departure from the normal proportions. The same has been seen by many hybridisers using animal types. But the further fact that there is a still greater variation in the statistical relations of the sexes in the *offspring* of hybrids, is rather favourable to the hypothesis.

The frequent occurrence of hermaphrodites among *first* crosses is also difficult to explain on the present hypothesis.]

7. *Reversions.*—With the Mendelian conception of the heterozygote as a form with its own special "*hybrid character*," we have a *rationale* of large numbers of "reversions"; for we already know many cases where heterozygotes do present the characters of putative ancestors. This fact reduces to harmony several groups of results where different experimenters, believing themselves to have worked with similar organisms, have reached seemingly contradictory conclusions. For some have used pure forms and others heterozygotes appearing in their guise.

THE NATURE OF ALLELOMORPHISM.

A. *Simple Allelomorphs.*

The following list enumerates the principal cases in which the phenomenon of allelomorphism has either been actually proved to exist or may be safely inferred from the published records.† In each of these cases more or less definite dominance of one character has been found, and in this list the dominant character is put first:—

1. Hairiness and absence of hairs (Lychnis).
2. Hoariness and absence of hairs (Matthiola).
3. Felted ears and smooth ears (Wheat).‡

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* 'Ann. Sci. Nat.,' vols. 16, 24, and 30; 1829, &c.

† [From the evidence of crosses kindly carried out for us by Mr. Leonard Sutton we are able to add the "palm" leaf (palmatifid) and reddish stems of *Primula sinensis* as dominant characters, while the "fern" leaf (pinnatifid) and purely green stems are recessive characters.—March, 1902.]

‡ Rimpau, 'Landw. J. B.,' 20, 1891, p. 346.

4. Prickliness and smoothness of fruits (Datura).
5. Style long and short (Œnothera).*
6. Beardless and bearded ears (Wheat and Barley).†
7. Pointed seed and rounded seed (Maize).‡
8. Round and wrinkled seed (Pisum).
9. Starch endosperm and sugar endosperm (Maize).
10. Inflated (generally hard) pods and constricted (generally soft) pods (Pisum, Phaseolus).
11. Axial distribution of flowers and terminal distribution of flowers (Pisum).
12. Tall habit and dwarf habit (Pisum, Phaseolus), to which, from experiments seen at Messrs. Sutton's, we think we may safely add tall habit and dwarf procumbent habit (known to gardeners as "Cupids") in Sweet Peas (*Lathyrus odoratus*).§
13. Entire petals and laciniated petals (*Chelidonium majus*).||
14. Normal zygomorphic form and peloric form (Antirrhinum¶ and probably Linaria).**
15. Normal habit and waltzing habit (connected with malformation of the aural labyrinth) (Mouse).††
16. Presence and absence of extra toe (Fowl).‡‡
17. Pea comb and single comb (Fowl).
18. Rose comb and single comb (Fowl).
19. Polled and horned breeds (Cattle and probably Goats).§§

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* De Vries.

† Rimpau, *loc. cit.*, pp. 341 and 353. Since this paper was written we have received Tschermak's valuable analysis of the phenomena in regard to wheat, which considerably extends our knowledge of allelomorphism in that species (see 'Ztsch. für d. Landw. Versuchswesen in Oester.,' vol. 4, 1901, p. 1029.

‡ Correns, 'Biblioth. Bot.,' vol. 53, 1901

§ Some distinct exceptions to the rule of dominance of the tall form are already known. [See final note.]

|| De Vries.

¶ Darwin, 'An. and Plts.,' ed. 2, vol. 2, p. 45.

** In the case of *Linaria*, Naudin found that on crossing a peloric *Linaria* with a normal one a mixture of normal and peloric plants resulted. As to the origin of the peloric parent there is no information, and consequently it may have been a heterozygote. See Naudin, 'Nouv. Arch. du Mus.,' 1865, I, p. 137.

†† Von Guaita, 'Ber. Natur. f. Ges.,' vol. 10, 1898, p. 317, and vol. 11, 1899, p. 131. For reference to this interesting case we are indebted to Professor Correns.

‡‡ The allelomorphism is not yet fully proved in this case. It is the only obviously meristic character in which there is yet any evidence of allelomorphism.

§§ It is almost certain that absence and presence of horns are allelomorphic characters. In England there are three principal polled breeds of cattle—the Aberdeen-Angus, Galloway, and the Red Polled. The first two are black, the last red. Between these and the horned breeds crosses are annually made in large numbers. This is especially the case with the Angus, from which great numbers of cross-bred cattle are annually bred for the meat market. These are usually Angus-Shorthorn crosses, but other horned breeds are also occasionally used. The

20. White shanks and yellow shanks (Fowl).
21. White plumage and general brown coloration (Fowl).*
22. Several coloured forms of flowers and their white varieties.
23. Several colours of fruits and their xanthic varieties (Atropa, Solanum).
24. Several colours of seed coats.
25. Darker and lighter colours of endosperm (Maize).
26. Yellow and green cotyledons (Pisum).

With regard to seed-colours, Correns has shown that the question is a complex one, depending on several factors. In Maize, especially, the seed-skin and the several parts of the endosperm may all be independently concerned in giving the net result. Each must be considered separately, and in several cases the dominance is imperfect, and blendings may occur.†

Between various simple allelomorphs correlations may of course occur. A few of these we know already. But in these cases of simple

cross between a pure Angus and a pure Shorthorn is almost always a blue-grey without horns. Generally the horns are represented by loose corns of horny material, sometimes imbedded in the skin and not rarely hidden by the hair. Such "scurs," as they are called in the north, are objected to in the pure polled breeds and are mostly absent.

Notes of the cross-breds exhibited at the Smithfield Club Cattle Shows in 1888, '89, '98–'01 give the following results. The animals are classified according to the descriptions in the Catalogue. No doubt, however, the actual purity of the parent breed or breeds was in many cases doubtful. Taken as they stand, the numbers exhibited in these six years were as follows:—

From $\left\{\begin{array}{l}\text{Polled Angus}\\ \text{Polled Galloway}\\ \text{Red Polled}\end{array}\right\}$ × some horned breed, usually Shorthorn, and the reciprocal cross—104 polled, 13 horned.

From first cross animals bred as above, mated with a pure polled parent—23 polled, 1 horned.

From first cross animals mated with some horned parent—18 horned, 24 polled.

When allowance is made for the very rough materials out of which these figures come, it is clear that the facts cannot be very far from the Mendelian expectation. It is, however, likely that the allelomorphs concerned are not merely the horned character in its entirety, and total absence of horns. For in the offspring of (polled × horned) × polled, the horns, when they occur, are often *loose* though of fair size. If all parts were completely correlated we should expect *either* absence of horns (perhaps mere scurs) *or* ordinary horns like those of horned breeds. Probably, therefore, there is not *complete* correlation between the formation of horns and that of the bony cores which carry them, and these characters are divisible in transmission. Unfortunately the cross-breds are practically never bred together, so the valuable evidence thus attainable is wanting. It should be mentioned that in offspring of (polled × horned) × horned the coat-colour character also breaks up.

* [Wh. Dorking × Ind. Game crosses are this year giving exceptions to dominance of white.—1902.]

† Full details given in Correns' memoir, 'Biblioth. Bot.,' 1901.

correlation the gametes may each transmit the correlated groups or the opposite allelomorph entire (see case of Matthiola, p. 81).

From the foregoing list it appears that allelomorphism may occur in a great diversity of characters, involving many different physiological factors.

In the plants albinism appears to be recessive, but in the case of fowls white plumage is dominant, though not completely so. It does not appear as yet that simple allelomorphism occurs between any two colours, of which neither is xanthic or albino.

B. *Compound Allelomorphs.*

So far, in all or nearly all the cases we have considered, the dominant and recessive characters are each *simple*. In other words, when the heterozygotes breed together, they produce dominants and recessives like their parents, heterozygotes like themselves, and no other forms. The gametes therefore respectively bear characters which are the same as those of the varieties which were used to produce the heterozygotes. We have next to consider a numerous and important group of cases in which a character of one of the original parental varieties after crossing is itself split up. Of these we will give illustrations.

1. *Sweet Pea.*—By the great courtesy of Messrs. Sutton and Sons we have been permitted to watch many of the experiments conducted at their nurseries. We cannot sufficiently express our indebtedness for the splendid opportunities of study in these fields thus provided. For the most part these phenomena are not dealt with in the present paper, and amongst many interesting results there witnessed we propose now to refer very briefly to the following only :—

Sweet Pea (Lathyrus odoratus).—Stanley, standard dark maroon or chocolate, with wings similar but somewhat tinged with violet, crossed with Giant White, gave *all* Giant Purple Invincible, viz., standards as in Stanley, but wings blue. These first crosses self-fertilised, gave Giant White, Giant Purple (without blue wings), Mars (a well-known red variety), Her Majesty (a full magenta, well known), and a form like Her Majesty, *but flaked with white*.*

One plant of each was saved and its self-fertilised seed sown. Mars and Her Majesty came true. The Giant White was tested, and it came true also. The Her Majesty flaked with white, however, gave Whites, Her Majesty, and Her Majesty flaked white again. The Giant Purple gave Giant White, Her Majesty, Giant Purples, and two plants of a streaky cream colour.

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* It is possible that this complex result does not always occur; for in another case a Giant Rich Purple, very like Stanley, crossed with Giant White, gave seedlings *all* Giant Rich Purple. These on self-fertilisation gave a mixture of Giant White and Giant Rich Purple again. One plant of each on self-fertilisation gave only offspring like itself.

The facts point to a higher degree of complexity than we can yet realise, but we see that the first crosses are all alike, though differing from the coloured parent. The same form, or something very like it, was often observed to come in other cases where a blue or purple parent was used in crossing. Now on self-fertilisation the first cross gave a variety of forms. It therefore produced a variety of gametes, not two kinds, but several. Of these forms some, Mars, Her Majesty (Giant White also in all probability), reproduced themselves exactly. Therefore they had only one kind of gamete, and they must be supposed to have been formed by the union of similar gametes. The purples, on the contrary, produced most of the whole series again, showing that they were producing a variety of gametes like the first cross parent itself.

Her Majesty flaked with white, gave some Her Majesty, some White, some Her Majesty flaked white. Therefore the flaked plants are heterozygotes, formed by the union of a Her Majesty gamete with a white gamete.

We are then led to the conclusion that the allelomorph transmitting the coloration of Stanley is *compound*, and that it can be broken up into simpler and possibly component elements. When *similar* elements, thus extracted, combine in fertilisation, they do not split up again on the formation of gametes. The constituents of the compound allelomorphs may perhaps be spoken of as *hypallelomorphs*.

The fact that Stanley did not occur again is another indication that its colour character had been broken up into *more than two* elements.

Another fact which may point in the same direction is that the purple formed on the first cross is different from that which recurs in the next generation. In fact, this Giant Purple Invincible results from the union of the whole compound allelomorph of Stanley with that of Giant White. We may suppose that it does not come again for the reason that the compound allelomorph has been broken up among the gametes borne by the first cross, and that the union of no two of these, or of any of them with white, results in that particular heterozygote form, Giant Purple Invincible. Inasmuch, however, as Giant Purple Invincible, not yet distinguishable from that produced in this cross, is a well-known and stable form, there must *either* be gametes corresponding to it* (or its male and female gametes must be dissimilar and combine in that definite heterozygote, which is most unlikely). Till the experiment has been repeated on a large scale we must not lay much stress on the absence of Purple Invincible after the break up of

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* Similarly from other crosses seen at Messrs. Sutton's it is clear that the form called "Painted Lady" may be another heterozygote form, though the same is one of the oldest and most familiar fixed forms. According to Mr. S. B. Dicks, there is good reason to believe the purple and the Painted Lady forms to be the oldest varieties. 'Report of Sweet Pea Conference,' 1900.

the first cross, because in other experiments where White Cupid (a procumbent form) was crossed with Mme. Carnot (a blue), Purple Invincible again resulted together with White Cupid (? the result of imperfect emasculation). These Purple Invincibles, self-fertilised, gave several forms, amongst them Mme. Carnot and some Purple Invincibles again. Whether this indicates that the compound allelomorph is not wholly broken up, or that its character may again be synthetically reproduced, cannot yet be said. Corroborative evidence that the blue elements are definitely extracted from the "derived" Her Majesty was seen in the fact that this variety when crossed with various pink and cream kinds gives no blues or purples.

To the whole subject of the results of crossing Sweet Peas we hope to return when our own experiments are further advanced.

The probability is that in this, as in other similar cases of compound allelomorphs, there is a heterozygote form which may be common to several combinations of dissimilar gametes, and it is characteristic of such forms that they may reproduce *in appearance* some putative ancestor. It is to this class of phenomena that Darwin's famous "reversions on crossing" are probably to be referred.

2. *Poultry.*—Another example of the splitting up of a compound allelomorph is probably to be seen in the poultry experiments. The first cross between Indian Game and White Leghorns, for instance, is white flecked with a few black or grey feathers, sometimes barred, sometimes irregularly marked with pigment. Such first crosses bred together give some dark birds and some light (see p. 108), the latter being sometimes pure white, sometimes flecked with black, and sometimes pile (brown and white). When White Dorkings are crossed with Brown Leghorns the result is very similar; but in each of these cases the dark birds resulting from the inter-breeding of the first crosses are not simply like their dark grand-parent, but belong to several distinct types of coloration such as black, cuckoo, silver-grey,* together with some more or less nearly reproducing the dark grand-parental type. The numbers reared are far too small to justify a comprehensive deduction, but that the types of coloration thus produced have some definiteness is quite clear. Whether any of them will breed pure must be unknown till next season. As already stated, some of these colours are already well known as characterising various breeds.

Until experiments have been carried out with the express object of proving the compound nature of allelomorphic characters and of resolving them into their constituents, we can only gather indications

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* The appearance of silver-grey in the offspring of first crosses between White Dorking and Brown Leghorn may be attributed to the certainty that White Dorking were related to Silver-grey Dorkings. The colour may, nevertheless, have come from resolution of the Leghorn colour, for it is not peculiar to Dorkings, but is known in other breeds, *e.g.*, Game Duckwings.

of such phenomena from experiments undertaken for other objects. Of these there are a considerable number which leave little doubt that further examination would disclose such a result. We may mention the observations of von Guaita on mice, from which it appeared that the first cross of albino mice with black-and-white Japanese waltzing mice, gave a grey house-mouse resembling in size, colour, and wildness the wild house-mouse.* The first crosses bred together gave albinos, grey mice, black and white, grey and white, and black mice (with the waltzing character distributed among them in proportions closely obeying the Mendelian ratio); of these the albinos produced, with one exception, albinos only when bred together. The grey marked with white, bred together, produced no more blacks or black-and-whites; and the blacks and the black and whites bred together gave no more greys, though both descriptions may still give albinos. Facts like these strongly suggest that, with suitable mating, the classes could be shown to consist of the original albino, and a number of forms, some of which would henceforth be pure, while others would be found to be heterozygous.

3. Another case, possibly of the same nature, is that of the Himalayan rabbit, of which an account is given by Darwin.†

The literature of pigeon-fancying abounds with information pointing to a similar *rationale* of the colour phenomena there seen. Formerly the recipes given in such treatises as to the methods of mating to be followed for the production of particular colours would have seemed mere nostrums, but now we can see at least the general basis of fact whence they have been derived.

The experiments with stocks described (p. 81) give cases probably also analogous. Several forms crossed together all gave purple for the first cross, which on being self-fertilised gave other colours in addition to those of the pure parental forms and that of the first cross.

This conception of compound allelomorphs is almost the same as that which Mendel himself introduces in speaking of his Phaseolus crosses.‡ His analysis does not, however, seem to be strictly correct, and the subsequent reasoning is consequently obscure and not altogether valid. He says if the colour of the red Phaseolus be made up of $A_1 + A_2 + \ldots$, then on crossing with a white form a, hybrid unions are produced, $A_1a + A_2a + \&c.$

But it is the group $A_1A_2 \ldots$ which is allelomorphic to a, and the heterozygote is $A_1A_2 \ldots a$, and not $A_1a + A_2a + \&c.$ It cannot be

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* Haacke, crossing albinos with grey-and-white Japanese waltzing mice, usually obtained the same result, viz., grey mice, but more rarely *black* mice. The latter result must be taken as indicating impurity in one or other parent. Vosseler, quoted by von Guaita, obtained greys only. See Haacke, 'Biol. Cblt.,' vol. 15, 1895, p. 45.

† 'An. and Plts.,' I, p. 113.

‡ *Loc. cit.*, p. 35.

till the crosses form their gametes that the compound allelomorph breaks up.

It is not evident how this error of expression came about. Mendel in consequence misses the point that by the breaking-up of the compound character after the cross, new fixed forms may be produced by union of the elements of the original compound allelomorph, without any admixture from the variety with which the first cross was made. Such pure forms may be represented as A_1A_1, A_2A_2, &c., and of these we have already seen instances in the case of the Sweet Peas, Mars and Her Majesty.

Of the coloured forms appearing as offspring of the first crosses inter-bred, some are compounded of colour-bearing gametes meeting similar or dissimilar colour-bearing gametes, and some (like the Sweet Pea, Her Majesty, flaked with white) of a colour-bearing gamete meeting a white-bearing gamete.

We have good reason to believe that the compound allelomorph is not in every case resolved into its ultimate constituents when the gametes of the first cross are formed, and indeed we must suppose such imperfect resolution to be present whenever, as in the case of the Sweet Pea, among the resolved forms (White, Mars, Her Majesty) there occur complex heterozygotes like Giant Purple, which can itself produce a series of forms in the next generation. Such a form may be represented as $A_2A_3 \ldots a$. It is to this class of complex heterozygotes that we conceive the Andalusian fowl to belong.

It is doubtful whether and in what sense we are entitled to regard the whole compound character as *one* allelomorph. Some justification for this conception is to be found in the fact that in the poultry crosses the light chicks bore to the *whole number* of dark chicks the proportions of 3 : 1. On the Mendelian hypothesis this must be taken to show that the cross-breds produce on an average white-bearing gametes equal in number to the whole number of colour-bearing gametes, which may bear the colour-allelomorph in various stages of resolution.

By statistical investigation of such cases it should be possible to determine with some success how the unresolved characters are related to the elementary characters, and to make a scheme of *equivalence*.

It is, perhaps, hardly too much to suggest that in a great number of cases the familiar fact so often observed that first crosses bred together give a profusion of new forms may be capable of similar explanation. With such new forms the usual experience is that some breed true from the beginning, while some continue to give rise to other forms, of which some may have already been produced, while others again are new. The cases we have taken are those of colour-varieties, as the facts in those cases are clearer, but their nature is probably not different. It is in this sense that crossing may be truly spoken of as a "cause" of variability, and some picture of that phenomenon is now provided.

The importance of this reasoning lies in the fact that we can now recognise that these different new forms may be, in their genetic composition, diverse. We are no longer to expect that it is a matter of chance whether each will be able to transmit any of the other forms, but we perceive that this is a question to be determined by actual observation once for all. When such determinations shall have been made on a statistical basis we shall be able to state precisely the numerical proportions which the gametes of the several classes bear to each other, and hence to determine the actual number of constituents of the compound allelomorph and their relationships to each other. This investigation is now merely a matter for precise quantitative analysis.

Remembering that we have no warrant for regarding any hereditary character as depending on a material substance for its transmission, we may, with this proviso, compare a compound character with a double salt, such as an alum, from which one or other of the metals of the base can be dissociated by suitable means, while the compound acid-radicle may be separated in its entirety, or again be decomposed into its several constituents. Though a crude metaphor, such an illustration may serve to explain the great simplification of the physiology of heredity to which the facts now point.

A marked feature in connection with compound allelomorphism* is the frequency with which in such cases one or more of the heterozygotes present what we have reason to regard as ancestral characters. To such "reversion" we referred in speaking of Sweet Pea crosses. The Sweet Peas produced a flower with purple standard and blue wings approaching what we may regard as a primitive Sweet Pea. Several white varieties of Stock produce a purple form; many of the crosses with the "half-hoary" type gave fully hoary heterozygotes. The Albino and Japanese mice produce a grey house-mouse as their heterozygote. *Why* such heterozygotes should show ancestral characters we do not know; but we can now recognise that such "reversions" are heterozygous mixtures and not constant forms. To speak of such reappearances of ancestral characters as a reappearance of the ancestral *form* is entirely misleading. These heterozygotes will not breed true, and *are* ancestral in no real sense. Not only are they heterozygous and in constitution compound, but, as in the Sweet Pea, several different compounds agree in having the same ancestral form as their specific heterozygote.

It is unfortunate that Darwin's own experiments with poultry and pigeons were so complex that it is now impossible to disentangle the results or to use them for the purposes of these deductions. He

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* There is no reason for supposing such reversion to be absent in all cases of heterozygotes formed by the union of *simple* allelomorphs, but the few clear cases known seem to be all cases including compound allelomorphs.

records the most complicated unions of birds of different breeds, some homo-, some hetero-zygotes, some exhibiting simple and others compound allelomorphs, and in the statement of results the all-important distinctions between the generations and the offspring of the several individual birds are often not observed.

To sum up the phenomena of compound allelomorphism, we may say that the evidence shows that the characters of a pure form when crossed with another may be broken up into component characters or hypallelomorphs, and that the decomposition may take place in various degrees of completeness.

To the variations which thus arise by resolution of compound characters we propose to give the name *Analytical Variations.* There can be no doubt that a very large proportion of the discontinuous variations in colour, at all events, met with both in wild and domesticated species are of this nature. The fact that similar component forms are similarly related to each other and to the type, in various species, thus provides the true account of numerous phenomena of "parallel" variation.

The facts thus grouped, suggest the following questions. Has a given organism a fixed number of unit-characters? Can we rightly conceive of the whole organism as composed of such unit-characters, or is there some residue—a basis—upon which the unit-characters are imposed? We know, of course, that we cannot isolate this residue from the unit-characters. We cannot conceive a pea, for example, that has no height, no colour, and so on; if all these were removed there would be no living organism left. But while we know that all these characters can be interchanged, we are bound to ask is there something not thus interchangeable? And if so, what is it? We are thus brought to face the further question of the bearing of the Mendelian facts on the nature of Species. The conception of Species, however we may formulate it, can hardly be supposed to attach to allelomorphic or analytical varieties. We may be driven to conceive "Species" as a phenomenon belonging to that "residue" spoken of above, but on the other hand we get a clearer conception of the nature of sterility on crossing.

Though some degree of sterility on crossing is only one of the divers properties which may be associated with Specific difference, the relation of such sterility to Mendelian phenomena must be a subject for most careful inquiry. So far as we yet know, it seems to be an essential condition that in these cases the fertility of the cross-bred should be complete. We know no Mendelian case in which fertility is impaired. We may, perhaps, take this as an indication that the sterility of certain crosses is merely an indication that *they cannot divide up the characters among their gametes.* If the parental characters, however dissimilar, can be split up, the gametes can be formed, and the inability to form gametes may mean that the process of resolution cannot be carried out. In harmony with this suggestion is the well-known experience of hybridisers, that if there is any degree of fertility in the first cross, with subsequent inter-bred generations the fertility may increase.*

Such increase in fertility is generally associated with some greater approximation to one of the parental forms. In terms of our hypothesis, we may conceive this fact as denoting that offspring formed of gametes which have successfully resolved the characters of the heterozygote, and are not bearers of the irresoluble characters, can form their own gametes with less difficulty.

That the sterility of hybrids is generally connected in some way with inability to form germ-cells correctly, especially those of the male, is fairly clear, and there is in some cases actual evidence that this deformity of the pollen grains of hybrids is due to irregularity or imperfection in the processes of division from which they result. It is a common observation that the grains of hybrid pollen are too large or too small, or imperfectly divided from each other.† Such conditions are what we should expect on the hypothesis here suggested.‡

However this may be, it would be of the utmost importance to discover at which of the divisions leading to the production of the gametes, the allelomorphic characters are divided. Correns has pointed out that the evidence of maize proves that in that case the two nuclei of the pollen tube must both be transmitters of the same character, for, in the fruit of the first cross between starch and sugar varieties, those seeds which have sugar endosperms produce pure recessive (sugar) offspring. This fact proves therefore that the nucleus which

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* Focke, 'Pflanzen Mischlinge,' p. 483; Gärtner, 'Bastarderzeugung,' pp. 333 and 373.

† See *e.g.*, Naudin, 'Nouv. Arch. du Mus.,' 1865, I, p. 95, and Wichura, 'Bastardbefruchtung im Pflanzenreich,' 1865, p. 37. Cases are easy to find.

‡ Remarkable observations bearing directly on this question have recently been published by Guyer ('Science,' vol. 11, 1900, p. 248), as to the spermatogenesis in hybrid Pigeons. The species used are not named, and the account is very brief. He states that in both sterile and fertile hybrids much variation in cell-division was seen, inequalities in chromatin distribution were common and multipolar spindles were abundant. In hybrid spermatogonia there were often more than eight (the normal number) large ring chromosomes. Sometimes there were sixteen small rings. In this case they usually located in two spindles, eight to each. Frequently both large and small rings were present. Guyer suggests, though apparently in ignorance of Mendel's work, that this phenomenon may indicate a "tendency in the chromatin of each parent species to retain its individuality." If so, he points out that in cells with two spindles and eight chromosomes, after division, some of the new cells will have chromatin from one parent and some from the other, and the observed "reversion" of the offspring of hybrids to parent species "may be due to the persistence of the chromatin of only one species in one or both of the germ-cells."

fertilises the embryo and that which fertilises the endosperm, are transmitters of the same character. Therefore, the separation of the characters does not take place in this case when the two generative nuclei divide from each other.* Further evidence on this question is wholly wanting. Several attempts are being made by others and by ourselves to determine this point by crossing varieties with recognisably different pollens; but, so far, the desired mixture of dissimilar gametes in our cross-bred has not been satisfactorily observed. As soon as some means shall have been found of making visible that differentiation which we now know must exist between the germ-cells of the same heterozygote, a vast field of research will be opened up. Till then, the microscopical appearances accompanying the segregation of the characters must remain unknown, and we are obliged to resort to the cumbrous and protracted method of deduction from the statistical study of the zygotes formed by the union of the several kinds of gametes.

Variation, especially discontinuous variation, of zygotes is in great measure thrown back on that of the gamete. We perceive, in fact, that the production of dissimilar gametes by one zygote may be compared, to take a rough illustration, to a bud-variation, constantly recurring in each heterozygote. Whether the divisions resulting in the formation of the dissimilar gametes are symmetrical or asymmetrical we cannot yet tell; but as in most cases of discontinuous variation, by sufficient searching, occasional instances, particular individuals or strains, will probably be found where the discontinuity is imperfect. As already pointed out also, the existence of exceptional gametes of a mosaic nature must already be inferred. It is unfortunate that so long as the statistical distribution of the zygotes is the only criterion by which the nature of the gametes can be deduced, even cases of impurity in extracted recessives—the readiest form in which imperfect differentiation will be seen—will not suffice to show whether there has been in fact such imperfect differentiation, or only defective dominance.

Mendel's discovery, it will be understood, applies only to the manner

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* Correns inclines to the view (based on the fact that pollen grains of crosses between forms of *Epilobium* differing in pollen colour do not show a mixture of the two parental colours) that the separation of characters does not take place when the pollen-grains divide from each other, but when the generative nucleus separates from the vegetative nucleus. Such an observation is, however, surely inconclusive. The pollen-grain is not the germ-cell, but the carrier of the germ-cell, and in any case there *may* be no universal correlation between the appearance of the pollen-grain and the characters it transmits. From what we know of discontinuous variation, and especially from the analogy of that "dichotomy" of characters seen in various parts of hybrids, we incline to the view that the separation of characters will be found to occur at various divisions in various forms. Information on these phenomena is given especially by Naudin, 'Nouv. Arch. Mus.,' I, 1865, p. 150; Focke, 'Oesterr. bot. Ztschr., 1868, p. 139; Macfarlane, 'Trans. Roy. Soc. Edin.,' 1895, vol. 37, p. 203.

of transmission of a character already existing. It makes no suggestion as to the manner in which such a character came into existence. The facts, however, leave no room for doubt that at least one character of each pair of simple allelomorphs has arisen discontinuously. The fact that the gametes of the cross transmit each member of the pair pure, is as strong an indication as can be desired of the discontinuity between them. From imperfection of the records, however, we cannot point to many cases where we know both that the origin was sudden, and that the characters obey Mendel's law, though no one practically acquainted with these subjects will feel any doubt that if those records were complete, there would be abundant evidence to this effect. A positive example, however, is that of *Chelidonium majus laciniatum*, of which the modern origin is recorded,* and the allelomorphic nature was proved by de Vries.† It is scarcely doubtful that such varieties repeatedly arise. The Cupid Sweet Pea is another (p. 140).

With regard to the compound allelomorphs, it must be determined by further investigation whether they similarly can come into existence in their entirety, or whether they are capable of synthesis. At present, though we can perceive the fact that they are capable of decomposition, we know nothing of the reverse process.

In the cases (p. 142) we have discussed, it is plainly the simple allelomorph that has discontinuously arisen.

While we can hardly doubt that, of each pair of simple allelomorphs, *one* must have come suddenly into existence, we cannot tell whether this fact means that something is *added* to the original organism, or whether, from the first, the appearance of the new character is to be regarded as a *replacement* of the corresponding character. For example, we do not know whether the greenness of the peas is due to an *addition* of something to the whole sum of the yellow pea, or to a *substitution* of something for the yellow character. We may partly understand the physiological nature of the yellowness and the greenness, or to take a clearer case, of the relation of the starch endosperm to the sugar endosperm, but this is as yet no help in elucidating the question. If it shall appear that the process is one of addition, the conception of the characters *splitting* may prove an incorrect one, and some other metaphor must be substituted.

Of special importance in this regard will be the study of cases where three or more characters are capable of mutual replacement. All cases studied so far are examples in which the allelomorphs are in *pairs*, but we know instances where three or more alternative forms of the organism occur, and an investigation of such cases may throw light on this part of the problem.

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* For literature see Korschinsky, Heterogenesis, trans., 'Flora,' Ergänzungsheft, vol. 89, 1901, p. 248.

† 'Ber. deut. Bot. Ges.,' 1900, p. 87.

Attention of those who propose to experiment in this direction must, however, be called to the fact that so long as we are dealing with simple allelomorphs, though there may conceivably be more than two forms of gamete (apart from "mosaics," &c.), in respect of each group of simple allelomorphs, yet each zygote can, variation apart, bear two only. Consequently, no zygote can be formed by the sexual process which shall be capable of bearing more than two forms of gamete of each sex. But it is not inconceivable that by grafting or some other form of union, a combination of three or more allelomorphs in one organism may be brought about.

Non-Mendelian Cases.—In the case of Matthiola and among the poultry, instances have been apparently found of definite departure from Mendel's law (pp. 81–6 and 107). It is certain that these exceptions at all events indicate the existence of other principles which we cannot yet formulate. But besides these cases there are three distinct classes of phenomena met with in breeding to which the Mendelian principles cannot be readily applied. It will be useful to consider briefly how each case departs from these principles, and whether by any modification they can be extended to such cases.

Such phenomena are—

1. The ordinary blended inheritance of continuous variations.
2. Cases in which the form resulting from the first cross breeds true.
3. The "false hybrids" of Millardet.

1. *Blended Inheritance.*—At first sight it seems that cases of continuous variations, blending in their hereditary transmission, form a class apart from those to which Mendel's principles apply. But, though it may well be so, the question cannot be so easily disposed of. The essence of the Mendelian conception is, as we have seen, that each gamete may transmit one allelomorph pure. So long as each heterozygote can only exhibit *one* allelomorphic character, the dominant, we can from a study of the heterozygotes and their offspring demonstrate the purity of the gametes. But dominance is a distinct and subordinate phenomenon. We readily perceive that the heterozygotes may show either of the parental characters discontinuously, or various blends between them, while the gametes which composed the heterozygotes may still be pure in respect of the parental characters. The degree of blending in the heterozygote has nothing to do with the purity of the gametes.

It must be recognised that in, for example, the stature of a civilised race of man, a typically continuous character, there must certainly be on any hypothesis more than one pair of possible allelomorphs. There may be many such pairs, but we have no certainty that the number of such pairs and consequently of the different kinds of gametes are altogether *unlimited* even in regard to stature. If there were even so few as, say, four or five pairs of possible allelomorphs, the various homo- and hetero-zygous combinations might, on seriation, give so near an approach to a continuous curve, that the purity of the elements would be unsuspected, and their detection practically impossible. Especially would this be the case in a character like stature, which is undoubtedly very sensitive to environmental accidents.

It is, of course, quite possible that the gametes in such cases do in fact vary as continuously as we see the zygotes do, but this cannot yet be affirmed. The great theoretical significance of this question should therefore lead us to suspend judgment for the present.

2. *First Crosses Breeding True.*—With respect to this phenomenon no experiments on a large scale have yet been made. Most examples are recorded in the form that A and B were crossed together and produced a third form, C. The C's were then bred together and some C's were again produced. We hardly ever are told that in this generation *only C's* were produced. Generally, however, we do not even know so much. The cases for example given by Darwin,* are for the most part general statements that certain new and now definite forms, the Swede turnip, for instance, were produced by crossing. Any such case may, therefore, be merely one of the resolution of compound allelomorphs followed by selection of the forms produced by the union of similar component allelomorphs. This, indeed, is probably the true account of most permanent forms produced by crossing.†

There remain, however, a few cases of which Mendel's‡ own crosses among Hieracia are a good example, in which a distinct form, produced by the first cross, has proved able to transmit its characters to its offspring. Of such cases we know very little. We may, perhaps, notice two features as apparently characteristic of these cases. First, that the results of the first cross may show no uniformity; secondly, that there is often a considerable degree of sterility.

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* 'An. and Plts.,' ed. 2, vol. 2, pp. 73–77.

† We cannot avoid expressing a doubt whether the wonderful series of "mutations" which de Vries has lately recorded ('Die Mutationstheorie,' 1901) as arising from *Œnothera Lamarckiana* do not fall under suspicion that they may owe their origin to some unsuspected original cross. Nothing can take away the extraordinary interest which attaches to these experiments, but until it has been shown in the clearest way that the *Lamarckiana* which gave rise to the "mutants" is a genuine uncrossed form we must feel hesitation in accepting the conclusion which de Vries has drawn from the facts.

This possibility is strengthened by the fact which Professor de Vries has told us, that the pollen of his *Lamarckiana* contains deformed grains, a point which is also mentioned by Pohl (' Oesterr. Bot. Ztschr., 1895, vol. 45, p. 212) in a paper to which de Vries refers (*loc. cit.*, p. 153).

On the other hand, we can scarcely suppose crossing to be the only cause determining the production of heterogeneous gametes, or in other words, variation in sexual descent.

‡ Mendel, 'Abh. Ver. Brünn.,' vol. 8, 1869. See also Swingle and Webber, 'Year-book Dept. Agric.,' 1897, p. 393.

In Correns' terminology such crosses are "homodynamous" and "homoögonous." De Vries speaks of them as "*erbungleich.*" In these instances the new form is able to give off gametes, male and female, carrying its own new character. Such facts plainly indicate a degree of complexity higher than that to which the Mendelian principles can apply, and for the present we have no insight into their nature.

3. *Millardet's* "*False Hybrids.*"—Some allusion must be made to the remarkable results described by Millardet,* which have been the subject of frequent discussion among practical evolutionists. Put briefly, Millardet found that when certain varieties, especially of strawberry, are crossed together, (1) the cross-breds may precisely reproduce the maternal type, without any indication of the paternal characters; (2) in other cases the cross-bred individuals may show *either* the maternal characters pure (save in one case the colour of fruits) *or* the paternal characters pure. Seeds from plants thus exclusively reproducing one parental type themselves gave plants again exclusively of that type. To such forms he gives the name "*faux hybrides*" or "*hybrides sans croisement.*"

In order to estimate the significance of these facts we ought to know of what variations the pure forms are capable, when bred *inter se*, without crossing. Upon this point we have as yet no evidence. If we assume that each of the forms used would, if bred pure, transmit its characters regularly to its offspring, then we should have established that the heterozygote produced exclusively gametes, transmitting the character which appeared as "dominant" in itself, and a new order of facts is thus revealed. It is difficult to see any escape from this conclusion, but, on the other hand, if it could be shown that the pure-bred offspring of the one form could themselves exhibit the characters of the other parent used in the cross, we should recognise that the parent forms themselves produced mixed gametes, and in such a case we should expect that when similar gametes meet in fertilisation the offspring resulting would breed true. On the whole this explanation is very improbable, but as yet it is not wholly excluded in some of the cases in which Millardet's phenomenon is alleged to have occurred.

In our experiments with Matthiola, cases were described which, it can scarcely be doubted, are fully proven. The same is true of some of de Vries' instances,† notably that of *Œnothera Lamarckiana* crossed with the *cruciata* var. of *biennis.* Possible instances occurred in regard to the combs of poultry (p. 122), though, as there pointed out, a simpler explanation is not altogether excluded in those examples. Such phenomena may perhaps be regarded as fulfilling the conception of Strasburger and Boveri, that fertilisation may consist of two distinct operations, the stimulus to development and the union of characters in the zygote.

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* 'Mém. Soc. Sci. Bordeaux,' sér. iv, vol. 4, p. 347.

† 'Ber. deut. Bot. Ges.,' 1900, vol. 18, p. 441.

[Note, added March, 1902.

Several times in the course of these pages, reference has been made to the phenomenon known as the "false hybridism" of Millardet. We are not aware that attempt has yet been made to elucidate that phenomenon. In view of the Mendelian discovery, we think it may not be althogether premature to suggest a possibility, which may perhaps be some guide to further experiment with this phenomenon.

In the false hybrid then, one or more characters are contributed to the zygote by one parent alone, to the exclusion of the corresponding character of the other parent. This exclusive character is exhibited on the development of the zygote; and that the opposite character is really excluded appears from the fact that the offspring of the "false hybrid" do not reproduce the excluded character.

The terms "false hybridism" and "false hybrid," though they have done good service, are clearly inconvenient for the fuller discussion that must arise respecting these facts, and we propose to denote the phenomenon by use of the term *monolepsis*, the ordinary result of fertilisation being distinguished as *amphilepsis.*

It is not yet certain whether monolepsis is a phenomenon peculiar to recessive characters; but while we are fairly sure that some of the cases in which it is seen are instances of recessive characters, we know no certain example of the monoleptic transmission of a dominant character. By the nature of the case, positive evidence of such transmission must be peculiarly difficult to obtain; for the first cross-bred generation would have to be individually tested on a considerable scale by subsequent breeding before such a possibility could be established.

Let us first consider certain features of the process of fertilisation as it may be supposed to occur between gametes bearing similar allelomorphs—for example, an R character. Each gamete bears R, the zygote exhibits it, and the gametes produced by that zygote bear it again.

But we note that we do not *know* whether the character exhibited by such zygote is really the product of the allelomorph of *both* gametes, or is due to the exclusive development of that of one gamete only. Commonly we conceive of all characters of a zygote as the product of both gametes, and in cases of true blended inheritance we must so conceive them. Such a view also accords well with all that we know of the visible processes of fertilisation. Nevertheless, the fact is not certain in the case of the union of similar gametes, and the case may —to take a rough and partially incorrect illustration—be comparable to the known fact that the faculty of speech is, in the normal case, controlled by the centre in the left hemisphere only, the corresponding structures presumed to exist in the right hemisphere not developing or at least not becoming functional. We do not *know*, in fact, whether the character in the zygote depends on, or is in any way affected by, the fact that *both* gametes were bearers of that character.

But if we suppose that the zygote character is thus a product of the two similar allelomorphs in the normal case, we may on that hypothesis form a conception of what may be imagined to take place in the case of monolepsis. For returning to the heterozygote we perceive that on the formation of its gametes there is a resolution or separation of the two dissimilar allelomorphs which came into it at fertilisation. May we not then suppose that in the case of the homozygote a similar separation takes place? The gametes of the heterozygote DR are bearers of D and R respectively separated out of DR; may not the gametes of the homozygote, which are bearers of R and R, receive those allelomorphs by a similar separation occurring between R and R?

If this reasoning prove valid, we suggest the possibility that in the case of false hybridisation the allelomorph is passed on from the zygote to the gamete without such resolution, and that thus it is not in a state which admits of its being affected by the contrary allelomorph of the other gamete. The case may perhaps be compared with the known fact that on separating the two segmentation spheres of an egg, each half may develop into a symmetrical larva.

Unproved as such a suggestion must necessarily be, it is in accord with several of the facts of crossing, of which no other account is as yet forthcoming. If, then, in a cross between D and R, an R be produced in circumstances which leave no doubt that such production is not due to mere environmental disturbance, we must suppose that the D character has never really "*met*" the R character.

Apart from examples of the appearance of a completely recessive form in the first cross, there are curious cases of the appearance of mosaic or pied forms in which the D and R characters form an irregular patchwork. In such a case Correns speaks of the characters as *pœcilodynamous*, a sufficiently expressive term. If, however, it were true that the pied condition is not really due to the dominance failing sometimes and succeeding sometimes, but to the existence in the mosaic of islands of the recessive character in the "paired" or unresolved state, we ought not to describe the phenomenon by reference to dominance at all.

In the introduction to this paper reference was made to the case of Canary—Goldfinch mules. Here the Goldfinch colour is normally dominant. It is said that, generally speaking, 99 per cent. of mules are thus "dark." As was also there stated, the belief is prevalent that in-breeding the hen Canaries has an effect in increasing the proportion of "light"—or canary-like mules. Others have disputed and denied the truth of this belief.

Nevertheless, it is generally admitted that to get "light" mules one should begin with a strain of Canaries which, on mating with the Goldfinch, throw some pied birds. On the hypothesis here suggested, the pied character is supposed to be due to the partially unresolved character of the recessive allelomorph. On in-breeding we may conceive the process of non-resolution on formation of gametes to be carried further. We have seen that cross-breeding leads to the fuller resolution of characters—in-breeding may lead to the contrary result.

With the Canary, as the mule is almost (if not quite) universally sterile, further experiment is impossible, but other cases are available for the experimental testing of this hypothesis.

If it is correct, it should appear that when on crossing a D and R a pied form is produced, showing patches of the R character, then such a pied form on crossing with the dominant again is more likely to give pied recessive or recessive offspring than a pure normal recessive would be, for we are on the hypothesis entitled to believe the gametes of the pied mule to partake of the same character as the zygote itself.

On the older view of breeding such a fact would be paradoxical; for the pied form, inasmuch as it already is part way to the D form, would be supposed *less* likely to show any R in its hybrid than the pure R form.

The fact that Tschermak in his crosses between the pea *Telephone* and yellow varieties obtained a considerable number of seeds greenish or patched with green, is consistent with this view; for this pea, though commonly a green or greenish pea, is liable to great variation, and is frequently mosaic or pied yellow and green.*

The remarkable series of Orchid crosses given by Hurst,† in which the female parent's characters alone appeared as the result of certain extreme crosses, seem rather to illustrate the possibility of parthenogenesis following the stimulus of fertilisation, without zygotic union.]

Galton's Law of Ancestral Heredity in relation to the new Facts.

Such a preliminary survey of the phenomena of heredity as we have attempted would be incomplete without some reference to this subject. We note at once that the Mendelian conception of heredity effected by *pure* gametes representing definite allelomorphs is quite irreconcilable with Galton's conception in which *every* ancestor is brought to account in reckoning the probable constitution of every descendant. With respect of each allelomorphic pair of characters we now see that only four kinds of zygotes can exist, the pure forms of each character, and the two reciprocal heterozygotes. On Galton's view the number of kinds is indefinite.

At first sight it may appear that as the two views are quite incompatible, they must relate to different classes of phenomena. In so far as

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* See Weldon, 'Biometrika,' I, 1902, Pt. II.

† 'J. R. Hort. Soc.,' xxiv, 1900, pp. 104–5.

Galton's law relates to continuous variations, with blended inheritance, this may be the case (see p. 152); but in some of the cases following Galton's rule, notably that of the colour of Basset hounds, the colours dealt with are discontinuous.* Let us consider what evidence there is in this case that the gametes are not pure tricolour *or* non-tricolour, as we should now expect them to be. The first question is, does either colour show dominance? If either were dominant it must clearly be the tricolour, and in view of the fact that both tricolour × tricolour and non-tricolour × non-tricolour are said to have given mixtures, neither colour can be supposed to be exclusively dominant. In this case, therefore, as it is impossible to tell which individuals are pure and which are heterozygotes, Galton's results might possibly have occurred, *and the gametes yet be pure.* More cannot be said without reference to the actual details out of which the tables were constructed.

Attention may also be called to the fact that in cases which fully obey Mendel's ratio (and exhibit dominance), two of the commonest matings happen to give the same result as they would do on Galton's expectation, though the latter is founded on wholly different considerations. Mendel, for instance, expects

DR × DR to give 3Ds and 1R,

and that DR × R will give equal numbers of Ds and Rs. Both these results are, *cæteris paribus*, to be expected on Galton's law, so that it might need a good deal of experiment to distinguish the two classes of cases. A clear distinction would, however, at once be found by comparing the result of DR × R with that of DR × D.

Bearing this in mind, and having regard to the considerations mentioned in the paragraph on blended inheritance, it is impossible to avoid the suggestion that Galton's law may be a representation of particular groups of cases which are in fact Mendelian, in the sense, that is, that there may be purity of gametes in respect of allelomorphic characters. In any case it is now certain that Galton's law cannot be accepted as "universally applicable to bi-sexual descent."

By any practical breeder this must have been always expected, for he knows that while he can rapidly fix some characters, some never come true at all, and others will not come true with any certainty after long selection. The expectation after simple selection is, in fact, quite different for different characters. Mendel's principle disposes of a great part of these difficulties, for we now know that any recessive

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* Pearson ('Roy. Soc. Proc.,' vol. 66, 1900, p. 142) has suggested a distinct formula for these cases of alternative inheritance, which he terms the "Law of Reversion." He urges that such phenomena should be treated separately from those of blended inheritance. Both laws alike are of course based on the numerical composition of the ancestry.

character may be fixed at once by selecting recessives, and that this fixity may have nothing to do with the novelty of the character, its "prepotency," &c., and that the heterozygote may never come true.

Galton's law in fact does not recognise that *absolute* purity which is so common a phenomenon in breeding, as it is in nature. The breeder, in hosts of instances, is not, as a matter of fact, constantly troubled by recurrences of forms with which, even in his own practice, his strain has been crossed. Of this the full explanation is now seen; for if two similar gametes meet, their offspring will be no more likely to show the other allelomorph than if no cross had ever taken place.

CONCLUSION.

We have now sketched the principal deductions already attained by the study of cross-breeding, and we have pointed out some of the results now attainable by that method. The lines on which such experiments can be profitably undertaken are now clear and a wide field of research is open.

The properties of each character in each organism have, as regards heredity and variation to be separately investigated, and, for the present, generalisation in regard to those properties must be foregone. The outlook, in fact, is not very different from that which opened in chemistry when definiteness began to be perceived in the laws of chemical combination. It is reasonable to infer that a science of Stoechiometry will now be created for living things, a science which shall provide an analysis, and an exact determination of their constituents. The units with which that science must deal, we may speak of, for the present, as character-units, the sensible manifestations of physiological units of as yet unknown nature. As the chemist studies the properties of each chemical substance, so must the properties of organisms be studied and their composition determined.

To the solution of the practical problems of heredity, and a determination of the laws of breeding both plants and animals, this is the first step. The attainment of these solutions is now only a question of time and patience.

That the same method will give the key to the nature of specific differences, we may perhaps fairly hope. Certain it is that until the several characters are thus disentangled and their variations classified, no real progress with this question can be expected.*

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* It is absolutely necessary that in work of this description some uniform notation of generations should be adopted. Great confusion is created by the use of merely descriptive terms, such as "first generation," "second generation of hybrids," &c., and it is clear that even to the understanding of the comparatively simple cases with which Mendel dealt, the want of some such system has led to difficulty. In the present paper we have followed the usual modes of expres-

[Since this Report was written, a paper has appeared by Professor Weldon, entitled "Mendel's Laws of Alternative Inheritance in Peas,"* questioning the importance of Mendel's discovery. This paper will be dealt with in a separate publication by W. Bateson, entitled "Mendel's Principles of Heredity," with which is incorporated a translation of Mendel's papers.—March 1902.]

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sion, but in future we propose to use a system of notation modelled on that used by Galton in 'Hereditary Genius.' We suggest as a convenient designation for the parental generation the letter P. In crossing, the P generation are the pure forms. The offspring of the first cross are the first filial generation F. Subsequent filial generations may be denoted by F_2, F_3, &c. Similarly, starting from any subject-individual, P_2 is the grandparental, P_3 the great-grandparental generation, and so on. We suggest this terminology here for the consideration of others who are working in the same field. All that is essential is to obtain uniformity, and it is quite likely that a better system may be suggested.

* 'Biometrika,' I, 1902, Pt. II.

[*Note to page* 140, "Cupid Sweet Pea."—Mr. Hurst called our attention to a passage in 'Report of the Sweet Pea Bicentenary Celebration, 1900' (published by Mr. R. Dean), p. 26, where it is stated that Mr. Laxton, of Bedford, crossed Cupids and tall forms, producing almost all *talls* on the first cross. Inquiry from Messrs. Laxton elicited the fact that in this Report the facts were by mistake inverted.]