THE FACTS OF HEREDITY IN THE LIGHT OF MENDEL'S DISCOVERY

Reports to the Evolution Committee of the Royal Society,
I, 1902, pp. 125-160

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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.[1] He crossed the peloric form with the normal and *vice versa.* The first crosses were all indistinguishable from the normal

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[1] *Animals and Plants, II,* p. 46, ed. 1885.

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 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 "homoögonous" 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 (R. p.12)[1] 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 unitcharacters existing in antagonistic pairs. Such characters we propose to call *allelomorphs,*[2] 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 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 (R. p. 23) that the otherwise pure extracted recessives (thornless) showed exceptionally a thorny patch or segment. Unless this is an original sport

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[1] [R. prefixed denotes pagination in original Report. En.]

[2] Correns speaks of the two opposite allelomorphs as a *Paarling.*

on the part of the individual, such a phenomenon may be taken as indicating that the germ cells may also have been mosaic.[1]

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 allelomorph 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, 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

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[1] 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.

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 (R. 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 crossbred. The want of dominance of hoariness in *Matthiola* seen in exceptional cases is a wholly different phenomenon (see R. 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,[1] 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.[2]

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

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[1] For examples see Fackenheim, *Jen. Zt.*, XXII, p. 343.

[2] 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 *cethiops,* etc. See Standfuss, *Handb. d. pal. Gross-Schmetterl.*, 1896, p. 305, *et seq.*

consists, in respect of each pair of allelomorphs, of *three*[1] *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. 61) 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.

1. *Heterozygous Forms.* It has long been known to breeders that certain forms cannot be fixed by selection indefinitely continued. In

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[1] Four, if reciprocal heterozygotes are not identical.

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.[1]

If two crested birds are bred together it is advised that they should have imperfect crests, in all probability another form of the heterozygote.[2]

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.[3]

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

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[1] The fancier’s view that the plain-head must be crest-bred is quite correct, because the heavy feathering (and perhaps skull-characters) are needed for a good crest. [Note from “corrigenda in Report I” published in Report II, 1905.]

[2] 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.*

[3] See also Lewis Wright, *Book of Poultry,* 1886, pp. 289 and 356.

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, though, doubtless, of a complex nature. 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),[1] and amongst plants the hybrids of *Digitalis.*[2] 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[3] acutely observes that the phenomenon of dissimilarity between the results of reciprocal crosses is more likely to be found among dioecious forms.

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[1] A good description of the differences between these forms is given by Cornevin, *Traité de Zootechnie,* 1891, p. 641.

[2] See Focke, *Pflanzen-Mischlinge,* 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.

[3] *Loc. cit.*, p. 228.

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 appear.

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,[1] 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.[2] 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. 46) 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

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[1] *Landw. Jahrb.*XX.

[2] Such a variety is Garton's Red King.

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.*[1] 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 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 dioecious 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.*

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[1] [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 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.]

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.

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.[1]

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 *Oenothera* 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

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[1] 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 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.

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.[1]

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 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.

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[1] 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.

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. 61) 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.

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,[1] suggesting that the differentiation of the spermatozoa of many insects and of some other Arthropods, 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*,[2] 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. 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,[3] it appeared that there is a more or less definite distribution of the sexes among the seeds of dioecious 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.

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[1] *Anat. Anz.* November, 1901, p. 220.

[2] Professor Miall has given me a reference to Cameron, *Phytoph. Hymenop., Ray Soc. Monogr.* I, p. 26, where authorities are quoted. He tells me that the same result was obtained in experiments of his own.

[3] *Ann. Sci. Nat.* XVI, XXIV, and xxx, 1829, etc.

The frequent occurrence of hermaphodites 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* o£ 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.[1] 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 cars and smooth ears (Wheat).[2]
4. Prickliness and smoothness of fruits (*Datera*).
5. Style long and short (*Oenothera*).[3]
6. Beardless and bearded ears (Wheat and Barley).[4]
7. Pointed seed and rounded seed (Maize).[5]
8. Round and wrinkled seed (*Pisum*).
9. Starch endosperm and sugar endosperm (Maize).

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[1] [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.]

[2] Rimpau, *Landw. Jahrb.* xx, 1891, p. 346.

[3] De Vries.

[4] 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 *Zisch. für d. Landw. Versuchswesen in Oester.* IV, 1901, p. 1029).

[5] Correns, *Biblioth. Bot.* LIII, 1901.

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*).[1]

14. Normal zygomorphic form and peloric form (Antirrhinum[2] and probably *Linaria*).[3]

15. Normal habit and waltzing habit (connected with malformation of the aural labyrinth) (Mouse).[4]

16. Presence and absence of extra toe (Fowl).[5]

17. Pea comb and single comb (Fowl).

18. Rose comb and single comb (Fowl).

19. Polled and horned breeds (Cattle and doubtfully Goats).[6]

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[1] De Vries.

[2] Darwin, *Animals and Plants,* ed. 2, II, p. 45.

[3] 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.

[4] Von Guaita, *Ber. naturf. Ges*. x, 1898, p. 317, and XI, 1899, p.131. For references to this interesting case we are indebted to Professor Correns.

[5] 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.

[6] 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 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 "sours," 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, 1889,1898-1901 give the following results. The animals

20. White shanks and yellow shanks (Fowl).
21. White plumage and general brown coloration (Fowl).[1]
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.[2]

Between various simple allelomorphs correlations may of course occur. A few of these we know already. But in these cases of simple

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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 Polled Angus or Polled Galloway or Red Polled × 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 sours) *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 that 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.

[1] [White Dorking × Indian Game crosses are this year giving exceptions to dominance of white. – 1902.]

[2] 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,* R. 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*.[1]

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

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[1] 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.

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.

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[1]. (or its male and female gametes must be dissimilar

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[1] 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

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 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 R. 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 grandparent, but belong to several distinct types of coloration such as black, cuckoo, silver-grey,[1] together with some

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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.

[1] 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 Dorkings were related to Silver-grey Dorkings. The colour may, nevertheless, have come from resolution of the Leghorn colour, for it is

more or less nearly reproducing the dark grandparental 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 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.[1] 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.[2]

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.

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not peculiar to Dorkings, but is known in other breeds, *e.g.* Game Duckwings.

[1] Haacke, crossing albinos with grey-and-white Japanese waltzing mice, usually obtained the same results, 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. Ctbl.* xv, 1895, p. 45.

[2] *Animals and Plants,* I, p. 113.

The experiments with stocks described (R. 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.[1] 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, $A_1a + A_2a$ + etc.

But it is the group A_1A_2 ... which is allelomorphic to a, and the heterozygote is A_1A_2 ... a, and not $A_1a + A_2a$ + etc. It cannot be 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, etc. 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 interbred, 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 ... 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

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[1] *Verh. naturf. Ver. Brünn,* 1865, vol. IV, p. 35.

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[1] is the frequency with which in such cases one or more of the heterozygotes present what we have reason to regard as ancestral

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[1] 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.

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 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 cases 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 interbred generations the fertility may increase.[1]

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

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[1] Focke, *Pflanzen-Mischlinge*, p. 483; Gäirtner, *Bastarderzeugung*, pp. 333 and 373.

too small, or imperfectly divided from each other.[1] Such conditions are what we should expect on the hypothesis here suggested.[2]

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 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.[3] Further evidence on this question is wholly wanting. Several

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[1] 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.

[2] Remarkable observations bearing directly on this question have recently been published by Guyer (*Science*, XI, 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 multi-polar 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."

[3] 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.

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 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

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Information on these phenomena is given especially by Naudin, *Noun Arch. Mus.* I, 1865, p.150; Focke, *Oesterr. Bot. Ztschr.* 1868, p. 139; Macfarlane, *Trans. Roy. Soc. Edin.* 1895, XXXVII, p. 203.

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,[1] and the allelomorphic nature was proved by de Vries.[2] It is scarcely doubtful that such varieties repeatedly arise. The Cupid Sweet Pea is another (p. 18).

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 we have discussed, it is plainly the simple allelomorph that has discontinuously arisen (cf. p. 13–14 above).

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.

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,” etc.), 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

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[1] For literature see Korsehinsky, Heterogenesis, trans. “Flora,” Ergänzungsheft, LXXXIX, 1901, p. 248.

[2] *Ber. Deut. Bot. Ges.* 1900, p. 87.

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 (R. 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,[1] 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.[2]

There remain, however, a few cases of which Mendel's[3] 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,

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[1] *Animals and Plants,* ed. 2, II, pp. 73-77.

[2] We cannot avoid expressing a doubt whether the wonderful series of "mutations" which de Vries has lately recorded (*Die Mutationstheorie,* 1901) as arising from *Oenothera 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, XLV, 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.

[3] Mendel, *Verh. naturf. Ver. Brünn,* VIII, 1869. See also Swingle and Webber, *Year-book Dept. Agric.* 1897, p. 393.

that the results of the first cross may show no uniformity; secondly, that there is often a considerable degree of sterility.

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,[1] 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 purebred 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,[2] notably that of *Oenothera Lamarckiana* crossed with the *cruciata* var. of *biennis*. Possible instances occurred in regard

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[1] *Mém. Soc. Sci. Bordeaux*, sér. IV, 4, p. 347.

[2] *Ber. Deut. Bot. Ges.* XVIII, 1900, p. 441.

to the combs of poultry (R. 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.

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 altogether 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 monolepsic 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 *poecilodynamous,* 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.[1]

The remarkable series of Orchid crosses given by Hurst,[2] 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.]

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[1] See Weldon, *Biometrika*, I, 1902, Pt. 2.

[2] *Journ. Roy. Hort. Soc.* XXIV, 1900, pp. 104-5.

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 Galton's law relates to continuous variations with blended inheritance, this may be the case (see p. 59); but in some of the cases following Galton's rule, notably that of the colour of Basset hounds, the colours dealt with are discontinuous.[1] 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

$$DR \times DR \text{ to give } 3\ D\text{'s and } 1\ R,$$

and that *DR* × *R will* give equal numbers of *D's* and *R's.* Both these results are, *coeteris paribus,* to be expected on Galton's law, so that it might need a good deal of experiment to distinguish the two classes of

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[1] Pearson (*Roy. Soc. Proc.* LXVI, 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.

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 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," etc., 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.[1]

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[1] 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," etc., 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 expression, 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, etc. 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.