CHAPTER X

EXPERIMENTAL STUDY OF INHERITANCE

As regards Mendel's Law, "The experiments which led to this advance in knowledge are worthy to rank with those that laid the foundation of the atomic laws of chemistry."—BATESON.

"The breeding-pen is to us what the test-tube is to the chemist—an instrument whereby we examine the nature of our organisms and determine empirically their genetic properties."—BATESON.

"That Hurst can predict the difference between the result of mating two pairs of rabbits externally identical, by means of a knowledge of the difference between their gametic constitutions acquired by previous breeding from them, constitutes, it seems to us, the longest stride the study of heredity has made for some time past."—*Nature*, lxxi. 1905, p. 315.

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§ 1. *Mendel's Discoveries*

IN *1866 Gregor Johann Mendel*,* *Abbot of Brünn, published* what some regard as one of the greatest of biological discoveries. After many years of patient experimenting, chiefly with the

* Gregor Johann Mendel was born in 1822, the son of well-to-do peasants in Austrian Silesia. He became a priest in 1847, and studied physics

edible pea, he reached a very important conclusion in regard to the inbreeding of hybrids, which is often briefly referred to as "Mendel's Law." His publication was practically buried in the *Proceedings of the Natural History Society of Brünn;* those who knew of it, as Nägeli for instance did, failed to realise its importance: in fact, Mendel's epoch-making work was lost sight of amid the enthusiasm and controversy which the promulgation of Darwinism (1858) had evoked. Mendel's Law seems to have been rediscovered independently in 1900 by the botanists De Vries, Correns, and Tschermak; and to Mr. Bateson we owe much, not only for his recognition of the far eaching importance of the abbot's work, but also for a notable series of experiments in which he has confirmed and extended it.

Mendel's Experiments.—What Mendel sought to discover was the law of inheritance in hybrid varieties, and he selected for experiment the edible pea (*Pisum sativum*). The trial plants, he says, must possess constant differentiating characters, and must admit of easy artificial pollination; the hybrids of the plants must be readily fertile, and readily protectable from the influence of foreign pollen. These conditions were afforded by peas, and twenty-two varieties or subspecies of pea were selected, which remained constant during the eight years of the experiments. Whether they are called species, or subspecies, or varieties, is a matter of convenience; the names *Pisum quadratum, P. saccharatum, P. umbellatum,* etc., do in any case represent groups of similar individuals which breed true *inter se.* It

and natural science at Vienna from 1851 to 1853. Thence he returned to his cloister and became a teacher in the Realschule at Brünn. It was his hobby to make hybridisation experiments with peas and other plants in the garden of the monastery, of which he eventually became abbot. Apart from two papers, one dealing with peas and a shorter one with hawkweeds, and some meteorological observations, he does not seem to have published much. But what he did publish, if small in quantity, was large in quality. He died in 1884.

should be noted that these peas have the particular advantage, for experimental purposes, that they are habitually self-fertilised —in North Europe, at least.

In studying the different forms of peas, Mendel found that there were seven differentiating characters which could be relied on:

1. The form of the ripe seeds, whether roundish, with shallow wrinkles or none, or angular and deeply wrinkled;
2. The colour of the reserve material in the cotyledons—pale yellow, bright yellow, orange, or green;
3. The colour of the seed-coats, whether white, as in most peas with white flowers, or grey, grey-brown, leather brown, with or without violet spots, and so on;
4. The form of the ripe pods, whether simply inflated, or constricted, or wrinkled;
5. The colour of the unripe pods, whether light or dark green, or vividly yellow, this colour being correlated with that of stalk, leaf-veins, and blossoms;
6. The position of the flowers, whether axial or terminal; and
7. The length of the stem, whether tall or dwarfish.

Mendel's Results: The Law of Dominance.—Having defined the differentiating characteristics of the varieties, Mendel proceeded to make crosses between these, investigating one character at a time. Thus, pollen from a pea of the round-seeded variety was transferred to the stigma of a pea of the angular-seeded variety, the stamens of the artificially pollinated flower being, of course, removed before they were ripe. The same was done all along the line.

What was the result in the hybrid or cross-bred offspring? It was found that they showed *one* of each pair of contrasted

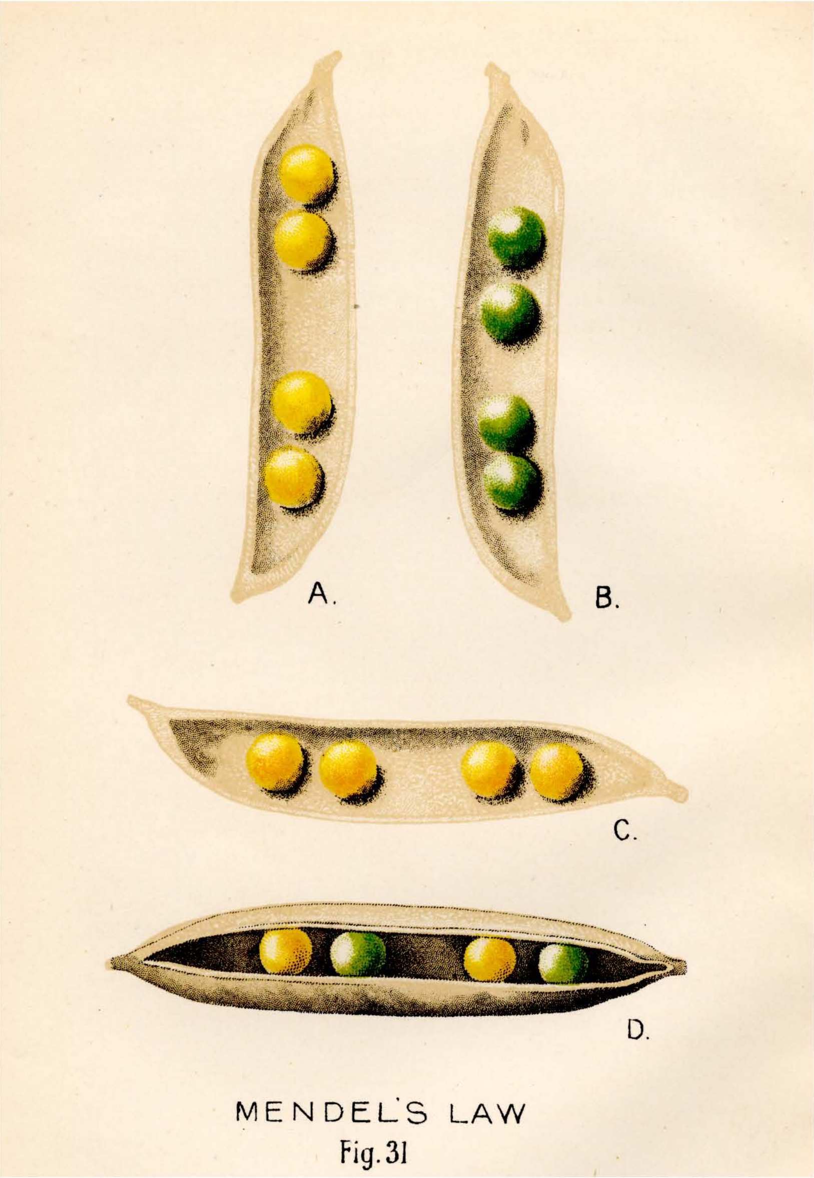

Fig. 31.—Peas showing Mendel's Law.

A, Pod of yellow-seeded (dominant) parent; B, Pod of green-seeded (recessive) parent; C, Pod of hybrid offspring—all with yellow seeds (F^1); D, Pod showing the splitting up of the next self-fertilised generation (F^2) into yellow-seeded and green-seeded.

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characters, to the total, or almost total, exclusion of the other. No intermediate forms appeared.

Mendel called the character that prevailed *dominant*, and the character that was suppressed, or apparently suppressed, *recessive*. And the first big result was that crosses between a plant with the dominant character and a plant with the recessive character yielded offspring all resembling the dominant parent as regards the character in question. Let us for shortness call the parents D and R, and the first result may be expressed in a simple scheme :

D♂ × R♀ D♀ × R♂

\\/ \\/

D D

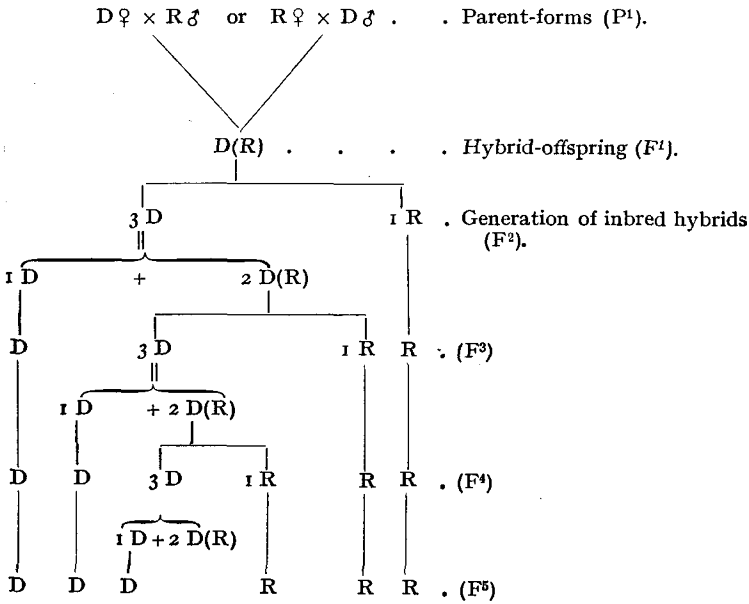
Thus, when tall varieties and dwarf varieties were crossed the offspring were tall. "Tallness" is the dominant character (D), "dwarfness" the recessive character (R).

The Law of Splitting or Segregation.—In the next generation the cross-bred plants (products of D and R, or R and D, but all apparently like D) were allowed to fertilise themselves, with the result that their offspring exhibited *the two original forms*, on the average three dominants to one recessive. Out of 1,064 plants, 787 were tall, 277 were dwarfs.

When these recessive dwarfs were allowed to fertilise themselves they gave rise to recessives only, for any number of generations. The recessive character bred true.

When the dominants, on the other hand, were allowed to fertilise themselves, they produced one-third of "pure" dominants, which in subsequent generations gave rise to dominants only; and two-thirds of cross-bred dominants, which on self-fertilisation again gave rise to a mixture of dominants and recessives in the proportion of 3 : 1.

The general results may be expressed in the following scheme :—



The result of the hybridisation is a generation (F^1) like the dominant parent. They may be represented by the symbol D(R), for they carry with them the possibility of having offspring with the recessive character; that is to say, the recessive character remains latent in the inheritance.

When these D(R)s are inbred (self-fertilised, in the case of peas) they have offspring (F^2), some of which resemble the recessive parent, while others resemble the dominant parent, and these occur in the proportion of 1 : 3. When those resembling the recessive parent are inbred, they breed true—*i.e.* they give rise to a line of pure recessives. Those resembling the dominant parent are all apparently alike, but their subsequent history shows that they may be divided into a set which breed true to the

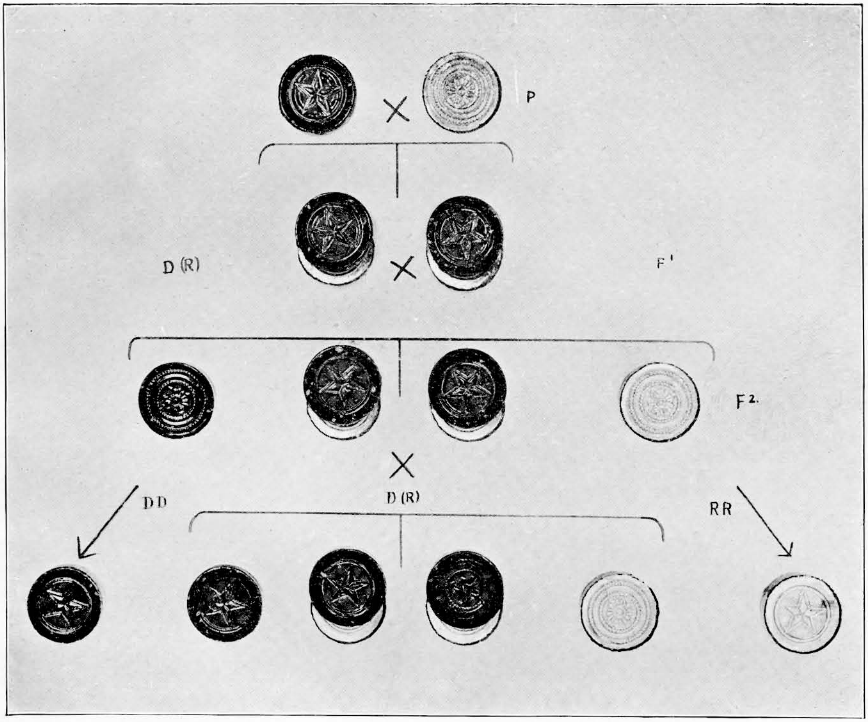


FIG. 32.—Diagram, photographed from draughtsmen, to illustrate Mendel's Law.

First line, (P) a black dominant and a white recessive. Second line (F^1) the hybrid offspring D(R), the black patent, the white latent below. Third line (F^2) one "pure" black, two "impure" blacks, and one "pure" white, 1DD + 2D(R) + 1RR. Fourth line pure extracted dominant to the extreme left, pure extracted recessive to the extreme right; in the middle, as usual, 1DD + 2D(R) + 1RR.

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dominant type and a set which behave like the first generation of hybrids—*i.e. they go on splitting* up *into dominant-like* forms and pure recessives. These two sets occur in the proportions of 1 : 2.

A Case of Peas.—Let us consider a concrete case. Peas with rounded seeds were crossed with peas having angular wrinkled seeds. In the offspring the character of roundness was dominant; the angular wrinkled character had disappeared or receded. It was not *lost*, as the next generation showed.

The hybrid offspring, all with rounded seeds, were allowed to self-fertilise. In their progeny roundish seeds and angular wrinkled seeds occurred in the proportions of 3 : 1. Here were the recessives again, and when *they* were allowed to self-fertilise they produced pure recessives only, with angular wrinkled seeds.

The dominants, however, were not all pure dominants, for when they were allowed to self-fertilise they produced one-third pure dominants and two-thirds "impure" dominants, the latter being distinguished *by the fact that in their offspring recessives* reappeared in the proportion of one recessive to three dominants.

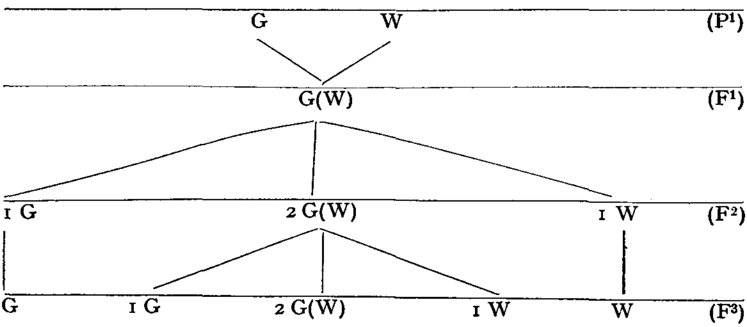
The outstanding facts, taking the case of yellow-seeded and green-seeded peas, may be thus summarised:—

Parental Generation (P1)	Yellow-seeded "pure" plant (dominant)			Green-seeded "pure" plant (recessive)	
First Filial (*Hybrid*) *Generation* (F1)	All the offspring were yellow-seeded. Self-fertilised they yielded				
Second Filial (*inbred*) *Generation* (F2)	Yellows (pure type)		Yellows *(impure type)*		Greens *(pure type)*
Third Filial (*inbred*) *Generation* (F3)	Yellows (pure type)	Yellows (pure)	Yellows (impure)	Greens (pure)	Greens (pure type)

Thus intercrossing of forms with contrasted characters results not in transitional blends, but in the *dominance of one* character and the recession of another. Self-fertilisation (the extreme of inbreeding) of the hybrids results in a number of pure recessives and a number of dominants in the proportion 1 : 3; some of these dominants (one-third) are pure, and produce only dominants ; some (two-thirds) are apparently pure, but produce dominants and recessives in the old proportion, 3 : 1.

A Case of Mice.—Let us take a concrete case from among animals. A grey house-mouse is crossed with a white mouse; the offspring are all grey. Greyness is dominant; albinism is recessive.

The grey hybrids are inbred; their offspring are grey and white in the proportion 3 : 1. If these whites are inbred they show themselves "pure," for they produce whites only for subsequent generations. But when the greys are inbred they show themselves of two kinds, for one-third of them produce only greys, which go on producing greys; while the other two-thirds, apparently the same, produce both greys and whites. And so it goes on.



Summary.—In his exceedingly clear exposition of Mendelism (1905) Mr. R. C. Punnett states the result thus: "Wherever there occurs a pair of differentiating characters, of which one is dominant to the other, three possibilities exist: there are recessives which always breed true to the recessive character;

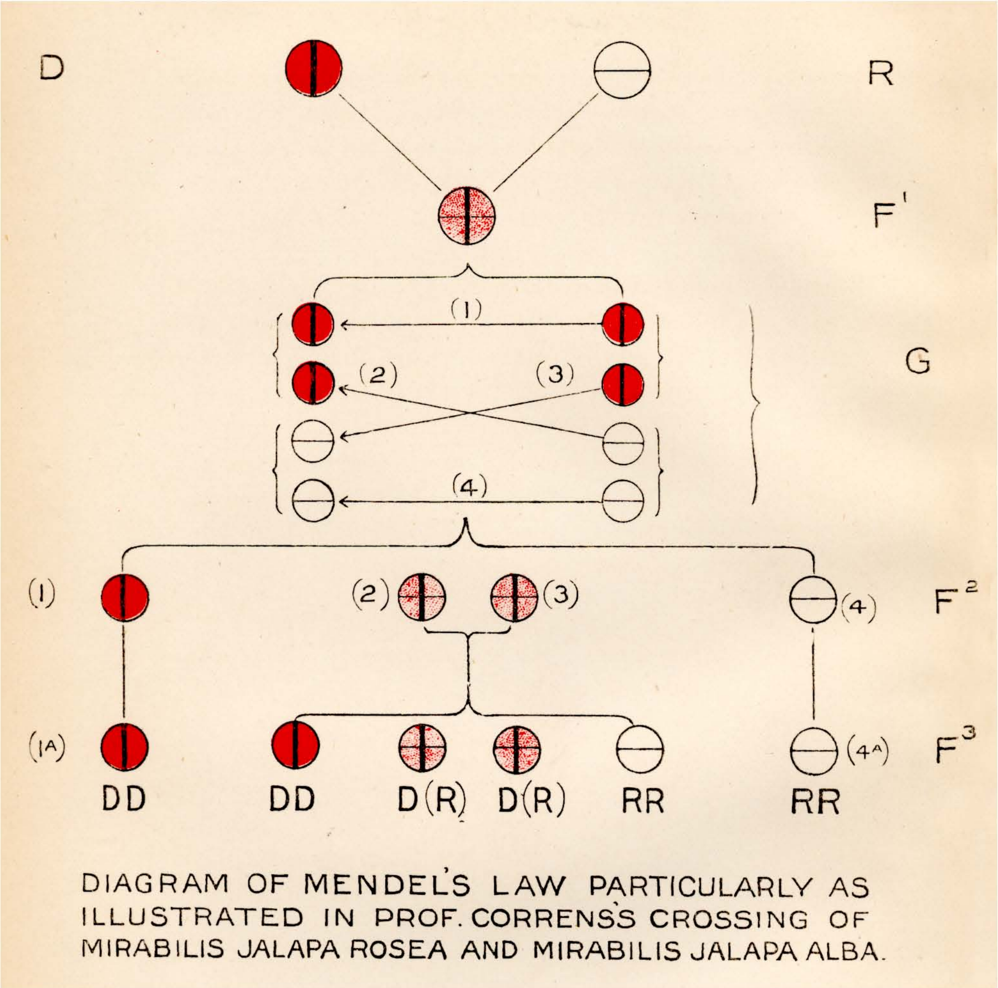


FIG. 33.—Diagram showing Mendelian inheritance in Mirabilis jalapa.

D, deep rose parent, *Mirabilis jalapa rosea*; the thick vertical stroke indicates dominance of the deep rose-colour. R, White parent, *Mirabilis jalapa alba*; the thin horizontal stroke indicates recessiveness of the white colour. F^1 Hybrid offspring, light rose D(R). The dominance of the rose was incomplete. G, Germ-cells hypothetically segregated into pure deep rose and pure white; their possible fertilisations indicated by arrows. The male cells are to the right, the female to the left. The fertilisation of two "homozygotes" or similar germ-cells indicated by the arrow (1) yields (1) in the next generation F^2—extracted pure dominant; the fertilisation of two "homozygotes" indicated by the arrow (4) yields (4) in the next generation F^2—extracted pure recessive. The fertilisation of "heterozygotes" indicated by the arrows (2 and 3) yield (2 and 3) in the next generation F^2—impure dominants, which being inbred (self-fertilised) split up in the next generation F^3 into deep rose, light rose, and white as before, in the proportions 1 : 2 : 1. Note also that 1 in the generation F^2 yields a pure dominant 1^A in the third generation F^3; and that 4 in F^2 yields a pure recessive 4^A in the third generation F^3.

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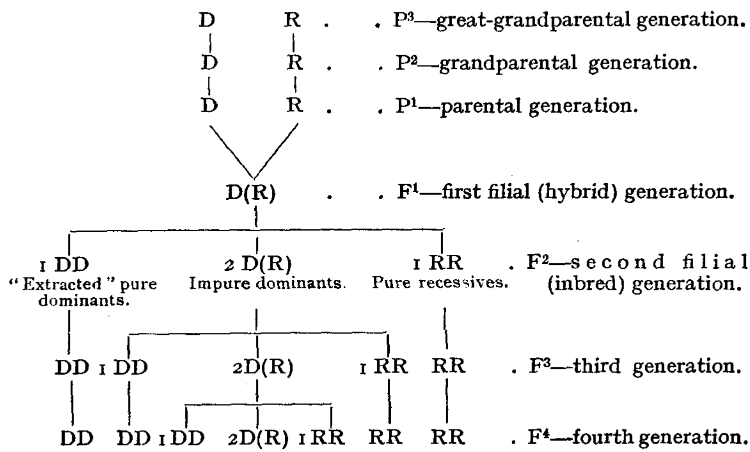
there are dominants which breed true to the dominant character, and are therefore pure; and thirdly, there are dominants which may be called impure, and which on self-fertilisation (or in-breeding, where the sexes are separate) give both dominant and recessive forms in the fixed proportion of three of the former to one of the latter."

Schematic Representation of Mendel's Law.—Following Mr. Punnett's suggestion, with slight modifications, we may use the symbols P^1, P^2, P^3 for the parental, grandparental, and great-grandparental generations; F^1 for the first filial (hybrid) generations; F^2, F^3, F^4 for the subsequent inbred generations. The symbol D(R) means a dominant with the recessive character unexpressed, but potentially present; DD or RR means pure "extracted" dominants or recessives—*i.e.* those pure forms which are sifted out from the inbreeding of "impure" dominants.



§ 2. *Theoretical Interpretation*

Mendel was not content with formulating his results in a law; he advanced a theoretical interpretation which is at once ingenious and simple.

Let us take the case of pea-plants with the quality of tallness or dwarfness, of round seeds or angular seeds, of coloured seed-coats or white seed-coats, of yellow or green cotyledons, or of

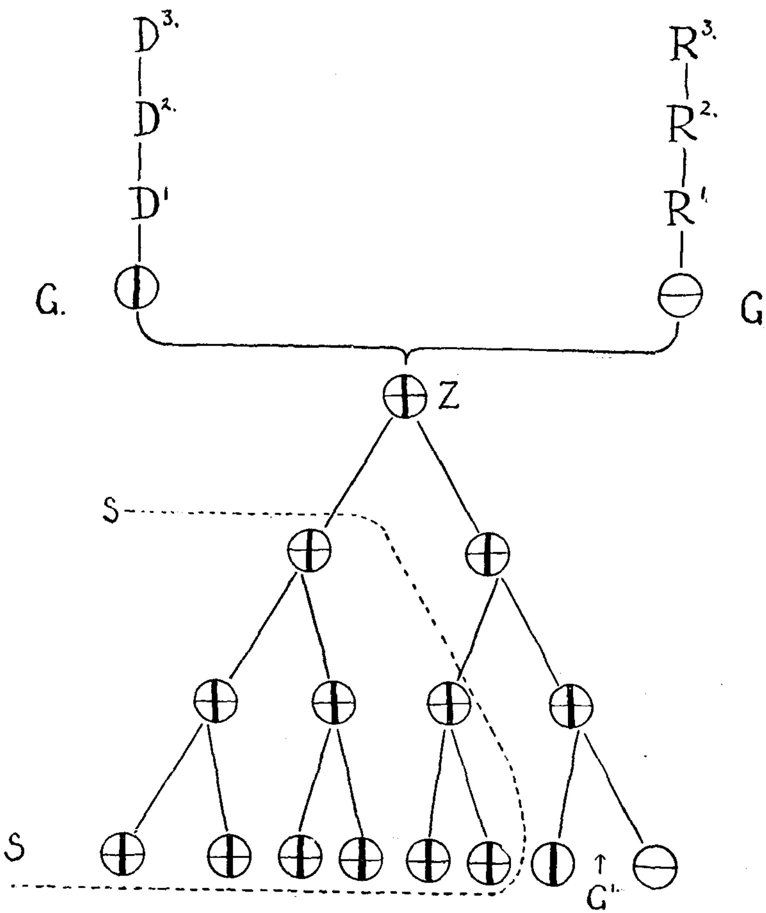


FIG. 35.—Diagram illustrating segregation of germ-cells.

D^1, dominant parent, its ancestry—D^2, D^3; R^1, recessive parent, its ancestry—R^2, R^3; G and G, germ-cells; Z, the zygote or fertilised egg-cell; enclosed in the dotted line S . . . . . .S, the somatic cells of the developing body; G^1 two germ-cells, one with a dominant character and one with a recessive character; dominance is indicated by the strong vertical stroke; recessiveness (latent in the body S . . . . . S) is indicated by the light horizontal stroke.

purple or white flowers (in each case, the *dominant* character has been named first). Let us assume that these are pure-bred varieties, well-established and breeding true, the tall form always producing tall offspring, the dwarf form always producing dwarf offspring, and so on. Let us also assume that the germ-cells contain material representatives of these "unit characters"—tallness, dwarfness, rounded seeds, angular seeds, yellow cotyledons or green cotyledons, purple flowers or white flowers.

The egg-cell of the tall pea is normally fertilised by a pollen-grain from the same pea, and the fertilised egg-cell develops into an embryo which becomes a tall pea. As the varieties breed true we assume that the only quality affecting dimensions which the germ-cells bear (*in expressible strength, at least*) is the quality of tallness.

But let us now take the case of a tall pea pollinated from a dwarf pea. The offspring become tall peas—the parent with the dominant character is prepotent. But the fertilised egg-cells which gave rise to these tall peas must have contained not only representative primary constituents corresponding to the quality of tallness; but also representative primary constituents corresponding to the quality of dwarfness. This quality of dwarfness is not expressed in development, but it must be present, as subsequent generations show; for when the egg-cells of the hybrids are self-fertilised they develop into offspring partly tall and partly dwarf. What Mendel suggested was that the hybrid produces in equal numbers *two kinds of germ-cells* (two kinds of egg-cells or two kinds of pollen-grains)—that there is in the developing reproductive organ a segregation of germ-cells into two equal camps, one camp with the potential quality of tallness, the other camp with the potential quality of dwarfness. Thus, if there are six ovules, three contain in their egg-cell the primary constituent corresponding to tallness, and three contain the primary constituent corresponding to dwarfness. Each of these is pollinated by a pollen-grain, which, by hypothesis, contains the potential quality of tallness or of dwarfness; and if the two kinds of pollen-grains are present in equal numbers, each ovule has an equal chance of being fertilised by a pollen-grain with a potential quality of tallness or by a pollen-grain with a potential quality of dwarfness. *Therefore* the result must be a set of offspring partly dominant and partly recessive, in the proportions of 3 : 1.

A schema will make the theory obvious:

D (*tall*) ♀ × R (*dwarf*) ♂

Egg-cell . ⦶ × ⊖ . Male-cell.

Fertilised egg-cell ⊕ This develops into an organism, whose body-cells express the quality "tallness" (D). The germ-cells of the organism segregate into two sets.

The mature egg-cells consist of two sets; half with the potential quality "tallness," half with the potential quality "dwarfness." ⦶ ⦶ ⦶ ⦶ ⊖ ⊖ ⊖ ⊖

⦶ ⦶ ⦶ ⦶ ⊖ ⊖ ⊖ ⊖ The mature male cells also consist of two sets, with the potential quality of "tallness" or of "dwarfness." What are the chances of fertilisation?

The result must be—

⦶ ⦶ ⊕ ⊕ ⊕ ⊕ ⊖ ⊖

i.e. 2 with the quality of tallness;

4 with the qualities of tallness and dwarfness;

2 with the quality of dwarfness.

In other words—

$$2\,D + 4\,D(R) + 2\,R;$$

or more generally—

$$n\,D + 2n\,D(R) + n\,R$$

But as the D(R) offspring are not distinguishable from the D offspring, until further breeding shows that they carry the recessive character in latent form, the proportion is—

3 dominants to 1 recessive.

Thus, Mendel assumed that in the hybrid D(R)—between a parent with a dominant character D and a parent with a homologous recessive character R—the germ-cells segregate into two

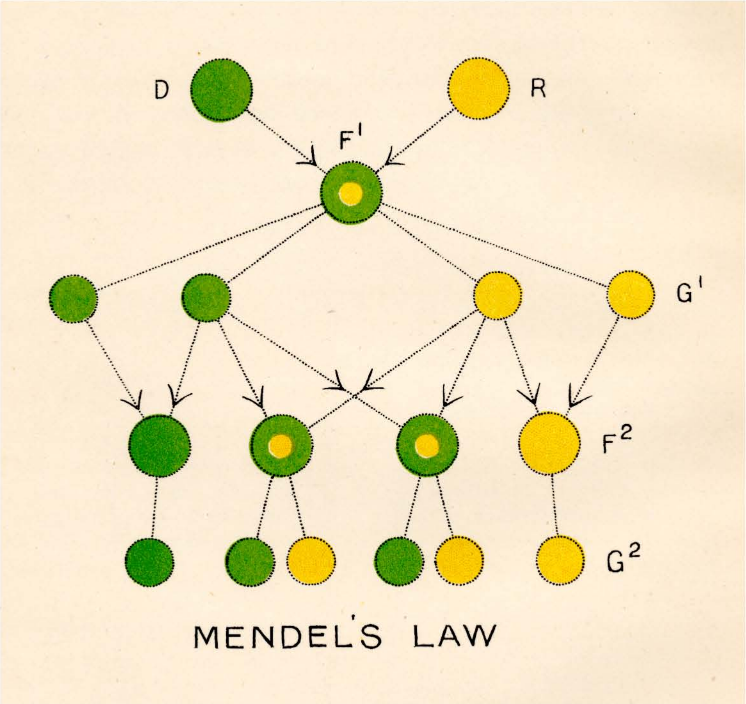


Fig. 34.—Diagram illustrating Mendelian segregation of germ cells.

D, dominant parent; R, recessive parent; F^1, hybrid offspring, the recessive character latent; G^1 the germ-cells of F^1, supposed to be segregated in two camps, green and yellow, with dominant and recessive characters. The arrows indicate possibilities of fertilisation Two greens may combine, producing pure dominant offspring—to the left. Two yellows may combine, producing pure recessive offspring—to the right. Green and yellow may combine, as at the start, yielding impure dominants—green enclosing yellow. G^2 ; this line indicates the kinds of germ-cells produced by the second generation F^2

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camps, one half containing the dominant character *in potentia* (d), and the other half containing the recessive character (r). This occurs in both males and females, so that when inbreeding takes place the possibilities are expressible thus:

D(R) produces 100 egg-cells	{ 50 with (d) 50 with (r)	50 with (d) 50 with (r) }	D(R) produces 100 sperm-cells

(1) 25 egg-cells (d) fertilised by 25 sperm-cells (d) = 25 fertilised gametes (d).
(2) 25 „ (d) „ „ „ (r) = 25 „ „ (dr).
(3) 25 „ (r) „ „ „ (d) = 25 „ „ (dr).
(4) 25 „ (r) „ „ „ (r) = 25 „ „ (r).

To sum up, 25 (d) developing into 25 pure D.
50 (dr) „ „ 50 D(R).
25 (r) „ „ 25 pure R.

Mendel's Theory summarised.—Mendel discovered an important set of facts, and he also suggested a theoretical interpretation—the theory of gametic segregation. As Mr. Bateson says, "The essential part of the discovery is the evidence that the germ-cells or gametes produced by cross-bred organisms may in respect of given characters be of the pure parental types, and consequently incapable of transmitting the opposite character; that when such pure similar gametes of opposite sexes are united in fertilisation, the individuals so formed and their posterity are free from all taint of the cross; that there may be, in short, perfect or almost perfect discontinuity between these germs in respect of one of each pair of opposite characters."

How the Segregation of Gametes might be effected.—Mendel assumed that the hybrid offspring (of two pure-bred parents differing markedly as to a unit character) produce two kinds of germ-cells, one kind with the dominant character, the other kind with the recessive character. This is the theory of the segregation of gametes into two sets of "pure" gametes, and, as we have seen, it harmonises well with the facts.

But it may be asked if there is any known process by which such a segregation could be brought about during the history of the germ-cells. Is it enough simply to say that the germ-cells are little living unities with an organisation, an equilibrium, of their own, and that they tend, as they multiply, to become more stable—namely, by separating out incompatibilities (dominant and recessive potential unit characters) and becoming the vehicles of either the one or the other? The adult organism cannot have both; intermediate forms or blends do not occur in these Mendelian phenomena. Are there differential divisions during the development of the germ-cells which lead to there being two camps of gametes which we may briefly describe as pure potential dominants and pure potential recessives? Is this not a possible expression of a struggle among hereditary items or homologous determinants, and in line with Weismann's theory of germinal selection?

A more precise suggestion, to which it seems too soon to attach great significance, is the fascinating hypothesis that the segregation occurs during the maturation divisions. If we assume that the chromosomes are the vehicles of the hereditary qualities, which seems highly probable; if we assume, further, that a particular potential unit character is contained in each germ-cell in one chromosome, and not in others, which seems a difficult assumption: then it is possible that Sutton may be correct in his suggestion that the segregation of gametes into two sets occurs in the course of the maturation divisions. (See T. H. Morgan, *Experimental Zoology*, 1907, p. 72.)

Is it necessary to assume a Segregation of "Pure" Gametes? —Mendel's theoretical interpretation of his results was based, as we have seen, on the fascinatingly simple assumption of the segregation of the germ-cells of the hybrid offspring into two contingents, each set the vehicle of only one of the two antithetic characters. To repeat the scheme:

D♀ R♂	D♀ R♂	. Pure-bred parents.
D(R)♂ producing sperm-cells,	D(R)♀ producing egg-cells,	. Hybrid offspring.
say 100 (D) and 100 (R),	say 100 (D) and 100 (R),	

Then, if the fertilisation is fortuitous, the possibilities are—

50 (D)(D) + 50 (D)(R) + 50 (D)(R) + 50 (R)(R),

resulting in adults in the proportion,

1 D + 2 D(R) + 1 R

But even if we suppose that the germ-cells are *all of one kind*—viz. with *both* dominant and recessive characters *in potentia*—but that in some the dominant primary constituents gain the ascendency and that in others the recessive primary constituents gain the ascendency, chance fertilisations might still result in the Mendelian kinds and proportions of offspring.

It may be that gametes which behave as if they were the vehicles of only one character have the other in reserve. For while purity means that only one character is expressed in development, it may be that the other character is there all the time in a latent state.

Prof. Weldon (1905) pointed to the analogy of two blastomeres, lying side by side in the 2-cell stage of the development of an ovum. Normally one blastomere will develop into all the right side, the other into all the left side of the embryo. They may be described as dominant in these respects. But a dislocation of the two cells may separate them, and each may develop into a complete embryo. In other words, characters which would in normal conditions have remained latent may as the result of some shock become patent. There are many exceptional results in Mendelian inheritance which suggest that the purity of the gametes is not so thoroughgoing as the theoretical Mendelian interpretation suggests.

Furthermore, with every desire to follow out the simplest line of interpretation, we must not forget that, even if all the fertilised ova started alike, with both dominant and recessive primary constituents, the expression of these in the course of development might result—especially if there be a real struggle among homologous determinants—in a victory here for the dominant characters, there for the recessive characters, and a sort of compromise in a third set.

But the exactness in the proportions of the three groups—1 D (pure dominants) + 2 D(R) (dominants with recessive character latent) + 1 R (pure recessives)—lends very strong support to Mendel's simple theory.

§ 3. *Elaborations*

Impure Dominants bred with Pure Types.—In the typical cases discussed above, a hybrid form D(R)—an impure dominant—is supposed to be self-fertilised or inbred. The results are according to the formula 1 DD (pure or extracted dominants) + 2 D(R) (dominant-recessives) + 1 RR (pure or extracted recessives).

But let us suppose the impure dominant or dominant-recessive D(R) to be bred with a pure type—*e.g.* RR (extracted recessive) (in technical phrase, a heterozygote unites with a homozygote). The impure dominant has, by hypothesis, equal numbers of two kinds of germ-cell—let us say, of egg-cell. The pure type has only one kind of germ-cell—let us say, of sperm-cell. The chances of fertilisation should be as follows:

n ⦶ + *n* ⊖ egg-cells of impure dominant;
n ⊖ + *n* ⊖ sperm-cells of pure recessive:

The result will be

n ova ⦶ fertilised by *n* sperms ⊖ = *n* offspring ⊕
n ova ⊖ fertilised by *n* sperms ⊖ = *n* offspring ⊖.

That is to say, equal numbers of impure dominants and pure recessives.

"This is what actually happens on crossing a fowl having a single comb (RR) with one having a heterozygous 'rose comb.'"

Or let us suppose the impure dominant D(R) to be bred with a pure dominant DD:

n ⦶ + *n* ⊖ egg-cells of impure dominant;
n ⦶ + *n* ⦶ sperm-cells of pure dominant:

The result will be *n* ⊕ + *n* ⦶ equal numbers of impure dominants and pure dominants.

"Here again experiment has borne out theory." Therefore, as Mr. Punnett says, "the generalisation known as the principle of gametic segregation may be regarded as firmly established on the phenomena exhibited by plants and animals when strains are crossed which possess pairs of differentiating characters."

Case of Paired Dominants and Paired Recessives.—A beautiful experiment was made by crossing a variety of pea with *Round* seeds and *Yellow* albumen (a pair of dominant characters) with another variety with angular seeds and green albumen (a pair of recessive characters). The result was offspring all like the dominant parent. These hybrids were inbred, and the results were some *Round* and *Yellow*, some *Round* and green, some angular and *Yellow*, some angular and green. (The dominants are represented by italics and capitals.)

RY ag

RY(ag)

Suppose the germ-cells segregate into the four possible kinds (say 100 of each):

(1) 100 RY (2) 100 Rg (3) 100 aY (4) 100 ag	which in inbreeding unite with four similar kinds	RY 100 Rg 100 aY 100 ag 100

What are the possible combinations (it being understood that form and colour represent a *pair* of characters—*i.e.* RR, Ra, etc., are impossible).

(1)

25 RY × 25 RY = 25 RY
25 RY × 25 Rg = 25 RY (g)
25 RY × 25 aY = 25 RY (a)
25 RY × 25 ag = 25 RY (ag)
= 100 RY

(2)

25 Rg × 25 RY = 25 RY (g)
25 Rg × 25 Rg = 25 Rg
25 Rg × 25 aY = 25 RY (ag)
25 Rg × 25 ag = 25 Rg (a)
= 50 RY + 50 Rg

(3)

25 aY × 25 RY = 25 RY (a)
25 aY × 25 Rg = 25 RY (ag)
25 aY × 25 aY = 25 aY
25 aY × 25 ag = 25 aY (g)
= 50 RY + 50 aY

(4)

25 ag × 25 RY = 25 RY (ag)
25 ag × 25 Rg = 25 Rg (a)
25 ag × 25 aY = 25 aY(g)
25 ag × 25 ag = 25 ag
= 25 RY + 25 Rg + 25 aY + 25 ag

The characters in brackets may be disregarded, since they behave as recessives to their correspondents. Thus the total is—

225 RY + 75 Rg + 75 aY + 25 ag
or 9 RY + 3 Rg + 3 aY + 1 ag

This actually corresponds with results obtained.

Dominance may not be quite Perfect.—In typical cases the hybrid is exactly like the dominant parent, as when the progeny of grey and albino mice are all grey. In other cases, however, the hybrid, while on the whole dominant, may show some influence of the recessive character, but not nearly enough to warrant us in speaking of a blend. Thus, when white (dominant) Leghorn poultry are crossed with brown (recessive) Leghorn, most of the offspring have some "ticks" of colour. When these are inbred they produce a quarter brown (extracted recessives) and three-quarters pure white or white with a few ticks. The dominance is not quite perfect, but this, Mr. Punnett says, "makes no difference to the essential feature of Mendel's discovery, which of course is the segregation of the dominant and recessive characters in the gametes" (1905, p. 27).

Blue Andalusian Fowls.—When black and white fowls are crossed there sometimes results a blue or Andalusian fowl "with a minute patchwork of black and white." When these are inbred they produce 25% black, 50% blue, and 25% white with black splashes. This splitting-up is characteristically Mendelian, but what gives rise to the "blue" feature is obscure.

The ingenious Mendelian interpretation in the case of the Andalusian fowl is that the black and the splashed white are the pure breeds, and that the blue Andalusian is a peculiar mongrel. We must refer to Mr. Punnett's essay on Mendelism for the interesting theoretical working out of the case, which is exceedingly instructive, since it shows that Mendelian interpretation is feasible even when the hybrid (the Andalusian) is quite distinct from either parent (black or splashed white).

Compound Allelomorphs.—A differentiating unit character capable of replacing another or of being replaced by another is technically called a *simple allelomorph*. But there are other differentiating characters which seem to consist of several components capable of being isolated and of entering into new combinations. These are called *compound allelomorphs*.

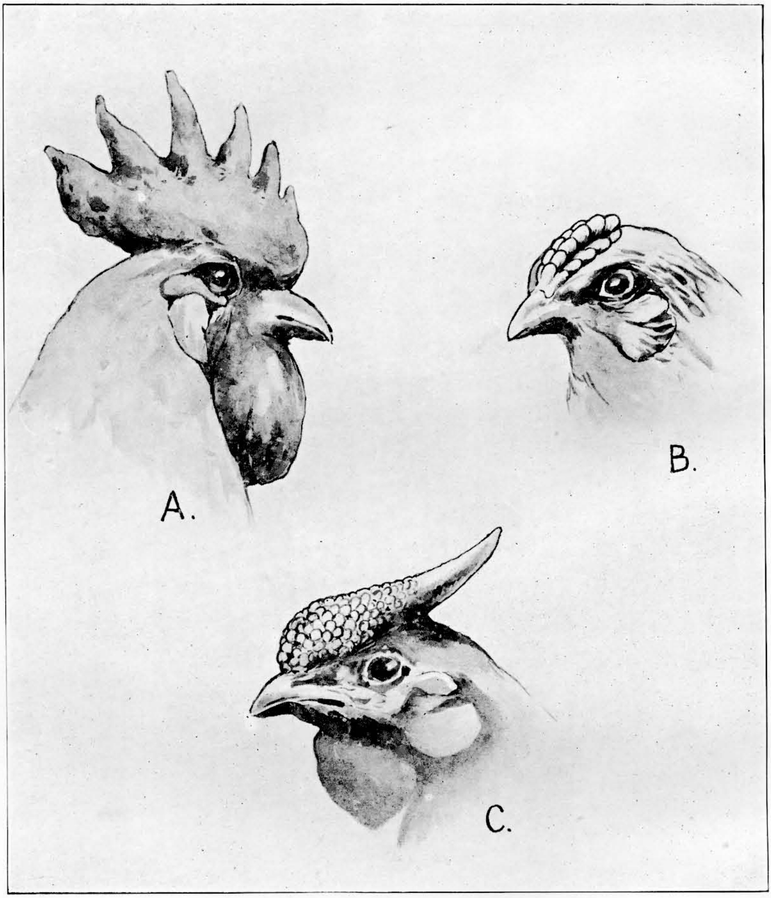

FIG. 36.—Combs of Fowls.

A, Simple serrated comb; B, Pea comb; C, Rose comb.

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Thus, to take Mr. Punnett's example, the "walnut" comb of Malay fowls—broad, flattened, corrugated like half a walnut, and with small bristle-like feathers posteriorly—becomes, as it were, a compound allelomorph. "This is shown by the fact that it may be synthesised from pure rose and pure pea. It behaves as a dominant to rose, pea, and single * combs. In a zygote formed by the union of walnut with rose or pea the walnut character is stable, and such heterozygotes form an equal number of gametes bearing the walnut, and either the rose or the pea allelomorphs. In other words, the compound allelomorph is stable in the presence of certain presumed simple allelomorphs. When, however, the zygote is formed by the union of walnut with single, the compound allelomorph would appear to undergo partial disintegration with the formation of walnut, rose, pea, and single allelomorphs in equal proportions. The zygote formed by the union of walnut with single is, so far as we at present know, precisely similar to that produced by the meeting of rose and pea" (Punnett, 1905, p. 40).

Sometimes pairs of characters go inextricably together, so that the breeder has not as yet been able to break their correlation. Thus, violet colour and hairiness in *Leucoja* go together, and so do whiteness and baldness in the same flower.

Some very difficult cases are known where the inbred hybrids have progeny some of which resemble one or both of the original parent types, while others resemble quite different types. Thus the Stanley variety of *Lathyrus odoratus*, crossed with the Giant White variety, yields Giant Purple, which, when inbred, has as progeny Giant White, Giant Purple, Mars, Her Majesty, and a new form.

Mr. Bateson interprets this kind of phenomenon as due to the analysis of a composite character into several sub-characters,

* A high serrated "*single*" comb is familiar in Leghorns, etc.; a flattened papillated "*rose*" comb with a posterior pike is seen in Wyandottes, etc.; a low "*pea*" comb, with three well-marked ridges, the median slightly higher than the other two, is characteristic of Indian game-fowl.

while others suppose that latent characters from previous pedigree are liberated by a departure from the usual routine of inbreeding.

Correns has investigated the interesting case of *Mirabilis jalapa*. The white variety, *alba*, crossed with the yellow variety, *gilva*, yields a hybrid with rose flowers and red streaks. When this is inbred the progeny include forms with white, red, rose, yellow, yellowish flowers, with or without various kinds of streaks. It requires some ingenuity to bring this within the Mendelian scheme, but Correns interprets it as due to the activation or liberation of disguised or latent characters.

Further Elaborations.—As experimentation has increased, the interpretations of the Mendelians have become more subtle. We may be allowed to illustrate this by a quotation from an admirable lecture delivered by Mr. Bateson in 1906 to the Neurological Society of London.

"A complication we often meet in the application of the rules of heredity lies in the fact that characters belonging to distinct allelomorphic pairs react on each other. A particular appearance, for instance, may depend on the coexistence of both C and R, and either of these factors alone may be unable to manifest any influence on the individual in the absence of the other. In that case there will be nine showing the appearance in question, say a colour, for seven which are without it. Or, again, the factor C may produce an effect alone; while R, though imperceptible in the absence of C, may modify the effect of C when C and R coexist. There will then be nine of the C + R class; three of the C class; and four all alike because C is absent, though their gametic composition is really diverse."

"For example, grey × albino rabbits gives grey F^1, with in F^2, three grey: one albino. But F^2 may be instead nine grey: three black: four albino. The latter result indicates that the factor which determines the colour to be grey was absent in the albino. The meaning of these occurrences was first pointed out by Cuénot."

" In certain plants we can go beyond this. Two white-flowered sweet peas, for instance, may when crossed give a coloured F^1, which by self-fertilisation will produce nine coloured, seven white. This result proves that the colour depends for its appearance on the coexistence of two complementary elements or factors."

" The nine contain both complementary factors C and R; the seven are three with C, three with R, and one with neither. Either factor alone is insufficient to cause colour. C and R are not allelomorphic to each other, but each is allelomorphic to its own absence." This conclusion has been tested and confirmed by an elaborate series of experiments made by Mr. Bateson, Mr. Punnett, and Miss Saunders.

" A further complication is due to the fact that colour, once formed by the meeting of the two complementary factors, is modified by the operations of distinct determining elements, just as is that of a rabbit. Thus, for instance, the nine coloured: seven white commonly forms the series twenty-seven purple: nine red: twenty-eight white."

" In the garden stock, which has formed the subject of a long series of experiments by Miss Saunders, a still further complication is met with."

" Colour in the stock, as in the sweet pea, requires the co-existence of two independent factors, each of which in the germ formation is allelomorphic to its own absence. In addition, the development of the hoariness or felting of hairs upon the leaves is also produced by another similar pair of factors, either of which alone may be present without a single hair being formed. But in the stocks employed (' ten-week stocks ') both these factors for hoariness may be present, but no hairs are developed *unless the flowers are coloured,* that is to say, unless the complementary pair which form pigment are also present."

We have ventured on this long quotation (1) because this book is meant to be a balance-sheet of facts and theories, and no *ex parte* statement; (2) because the increased subtlety of

Mendelian interpretation has an experimental, not a speculative basis; (3) because if these elaborations are justified we are led to caution in denying Mendelian inheritance in cases where its absence is only apparent; and (4) because the added conception of allelomorphs or contrasted unit characters working in pairs, abetting or counteracting one another, seems to us to bring the Mendelian theory into close approximation to the Weismannian conception of the struggle and interaction and co-operation of determinants.

Mendel's Results summarised.—1. The first result was the demonstration of the law of dominance, D × R = D(R).

2. The second result was the demonstration of the law of the splitting or segregation of the offspring of inbred hybrids into forms showing the dominant character and forms showing the recessive character, with on the average definite proportion (3 : 1) between the two sets: D(R) × D(R)=1 DD + 2 D(R) + 1 RR.

3. The third result was the conception of alternative pairs of "unit characters" (Bateson's allelomorphs), which behave in inheritance as if they were discrete unities.

4. The fourth result was the theoretical interpretation of the second, as due to segregation of the gametes into two equal groups, one bearing the dominant character and the other bearing the recessive character.

§ 4. *Illustrations of Mendelian Inheritance*

How far has Mendel's Experience been confirmed?—There has been confirmatory work by Correns (on peas, maize, and garden-stock), by Tschermak (on peas), by De Vries (on maize, etc.), by Bateson and his collaborators (on a large variety of organisms), by Darbishire (on mice), by Hurst (on rabbits), by Toyama (on silk-moths), by Davenport (on poultry), and so on. There are some difficulties and not a few discrepancies, but, as Bateson says, "the truth of the law enunciated by Mendel is

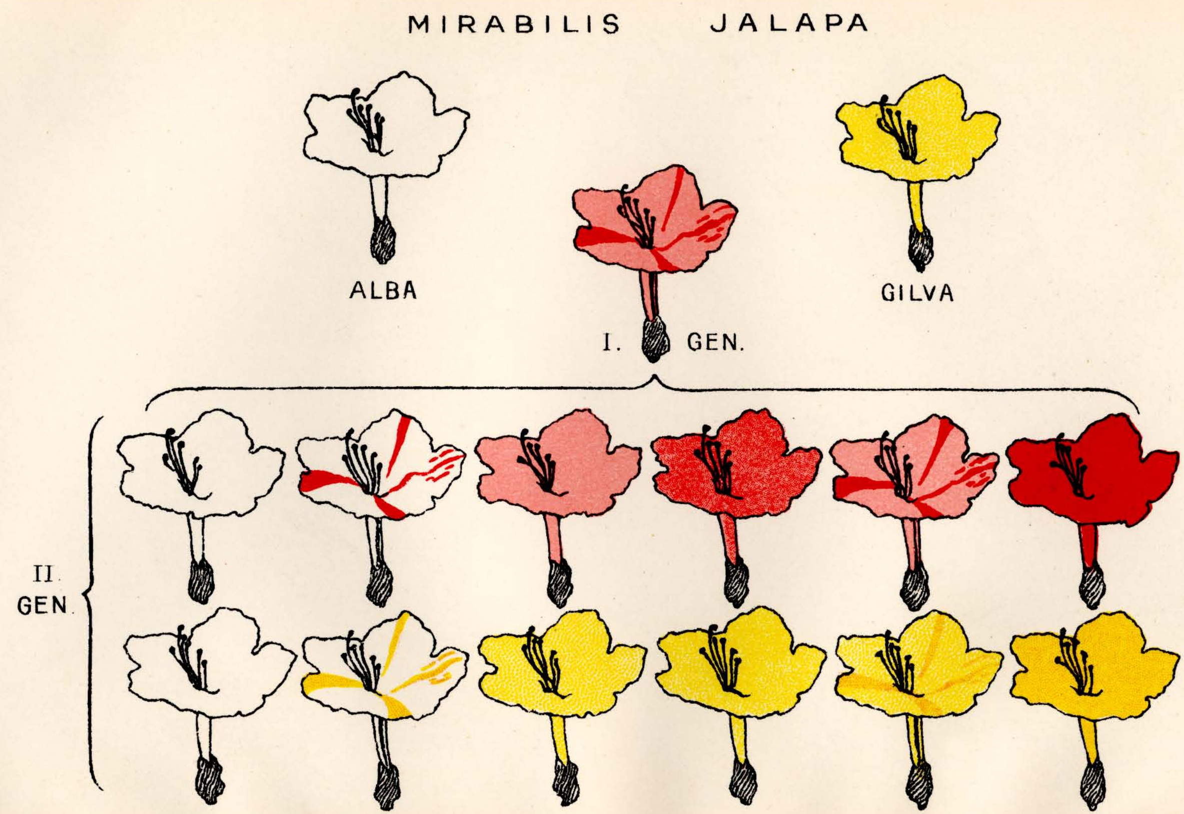

Fig. 37.

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FIG. 37.—Hybridisation in Mirabilis jalapa. (By kind permission of Prof. C. Correns.) Mirabilis jalapa alba is crossed with Mirabilis jalapa gilva. The hybrid offspring are light rose with red stripes (1. Gen.). When these are self-fertilised there are in their progeny no fewer than eleven kinds of flowers—namely, white, white with red stripes, light rose, deep rose, light rose with red stripes, red, white with yellow stripes, light yellow, yellowish, light yellow with darker stripes, and deep yellow.

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now established for a large number of cases of most dissimilar characters."

In experimenting with *Lychnis*, *Atropa*, and *Datura*, Bateson and Saunders found that the phenomena conformed with Mendel's law "with considerable accuracy, and no exceptions that do not appear to be merely fortuitous were discovered. In the case of *Matthiola* (garden stock), the phenomena are much more complex. There are simple cases which follow Mendelian principles, but others of various kinds which apparently do not. The latter cases fall into fairly definite groups, but their nature is obscure."

In experiments with poultry, the phenomena of dominance and recession were detected; interbreeding of the hybrid offspring resulted in a mixed progeny, "some presenting the dominant, others the recessive character, in proportions following Mendel's Law with fair consistency, though in certain cases disturbing factors are to be suspected."

The general result, so far, is that Mendel's Law has received confirmation in a number of very dissimilar cases.

Dominant and Recessive Characters.—Let us first of all collect a number of instances of contrasted characters which behave in relation to one another as dominants and recessives.

	Dominant.	*Recessive.*
	Tallness.	Dwarfness.
Pisum	Round seeds	Wrinkled seeds.
sativum	Coloured seed-coats.	White seed-coats.
	Yellow albumen in cotyledons.	Green albumen in cotyledons.
	Purple flowers.	White flowers.
Sweet pea.	Tall ordinary form.	Dwarf or "Cupid" variety.
	Coloured.	White.
Stocks.	Coloured.	White.
Wheat and barley.	Beardless.	Bearded.
	Later ripening Rivett wheat	Early ripening Polish wheat.
	Non-immune to "rust."	Immune to "rust."

	Dominant.	*Recessive.*
Maize.	" Starch " seed.	" Sugar " seed.
Nettles (*Urtica pilulifera* and *U. dodartii*).	Serrate leaf margin.	Entire leaf margin.
Mirabilis jalapa and *M. rosea*.	Rose colour.	Other colours.
Mice.	Coloured coat. Normal.	Albino coat. " Waltzing " variety.
Rabbits.	Coloured coat. Angora fur.	Albino coat. Short fur.
Poultry.	" Rose " comb of Hamburghs and Wyandottes.	High serrated " single " comb of Leghorns and Andalusians.
Cattle.	Hornlessness.	Horns.
Snails.	Bandless shell.	Banded shell.

Other Instances in Plants.—As is well known, there are two almost equally common forms of wild primrose: (A) thrum-types, with short styles and with anthers at the top of the corolla-tube; and (B) pin-types, with long styles and with anthers half way down the tube. The thrum-type is dominant over the pin-type.

The original species of Chinese primrose (*Primula sinensis*) has a palmate leaf. About 1860 a sport arose (from seed) which had a pinnate or " fern " leaf. The palmate form is dominant, and the fern leaf is recessive.

The deformed " Snapdragon " variety of sweet pea behaves as a recessive to the normal type.

The 2-row barley has certain lateral flowers which are exclusively staminate; in 6-row barley all the flowers are staminate and pistillate, and all set seed. Mr. Biffen crossed these forms, and found that the more negative character was dominant. The offspring were 2-rowed.

Maize.—When the common or starchy round-seeded maize is crossed with the wrinkled-seeded sugar-maize, the round starchy character dominates. When an egg-cell of the wrinkled sugar-maize stock is fertilised by a pollen-cell of the round starchy stock, the result is a round seed with starchy endosperm. If this seed is sown, it becomes a plant which, on self-fertilisation, forms a cob with a mixture of round starchy and wrinkled sugary seeds in the ratio 3 : 1. The wrinkled seeds yield sugar-

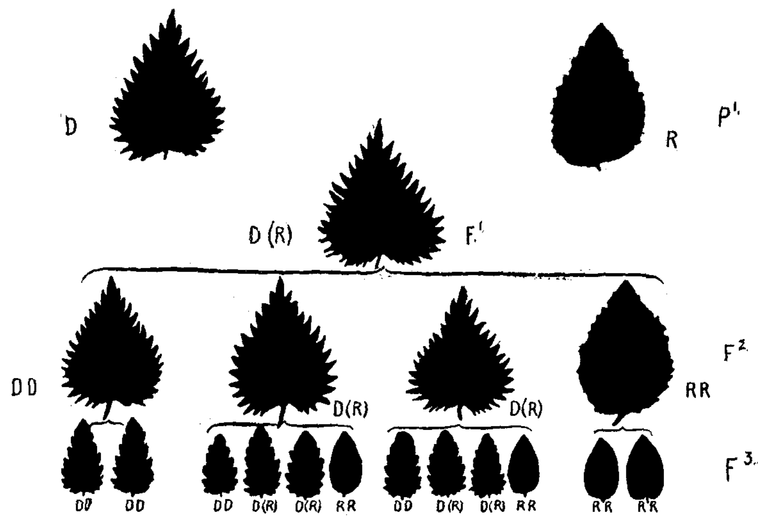

FIG. 38.—Diagram showing Mendelian phenomena in nettles. (By permission of Prof. Correns.)

P^1, leaves of the two parents; D, Urtica pilulifera; R, Urtica dodartii; F^1, leaf of the progeny, D(R), the serrated type being dominant; F^2, leaves of the hybrid's offspring; 1DD + 2D(R) + 1RR; F^3, leaves of the next generation; DD, pure extracted dominants; RR, pure extracted recessives; D(R), impure dominants.

maize; the round seeds yield two "impure rounds" to one "pure round." Correns has observed a very interesting case in which two pairs of contrasted characters are implicated.

One variety, *Zea mays alba*, which has *smooth* white seeds, was crossed with another variety, *Zea mays coeruleodulcis*, which has wrinkled *blue* seeds. The hybrids (F^1) had *smooth* *blue* seeds, one character of each parent being dominant, and one character of each parent being recessive. The hybrids were inbred, and the progeny (F^2) showed four combinations—*smooth blue*, *smooth* white, wrinkled *blue*, and wrinkled white (the dominant characters are italicised).

In the next generation (F^3), the wrinkled white, inbred, yielded wrinkled white—a case of extracted recessives breeding true. The *smooth* whites and wrinkled *blues*, inbred, yielded partly forms like themselves and partly wrinkled white. The *smooth blues*, inbred, yielded the same combinations as in F^2.

A finer corroboration of Mendelism could hardly be wished.

Nettles.—Correns crossed two "species" of stinging-nettle, *Urtica pilulifera* L. and *U. dodartii* L., which resemble one another except as regards leaf-margin, strongly dentate in the former, almost entire in the latter. The hybrid offspring (F^1) have all dentate leaves like the male or the female parent, as the case may be. *The dentate character is absolutely dominant.* The inbred (self-fertilised) hybrids produce offspring (F^2) of two kinds, with dentate and with entire margins, on an average in the Mendelian proportion, 3 : 1.

Immunity to Rust in Wheat.—Some kinds of wheat are very susceptible to the fungoid disease known as "rust"; others are immune. The quality of immunity to rust is recessive to the quality of predisposition to rust.

"When an immune and a non-immune strain are crossed together the resulting hybrids are all susceptible to 'rust.' On self-fertilisation such hybrids produce seed from which appear dominant 'rusts' and recessive immune plants in the expected ratio of 3 : 1. From this simple experiment the phrase 'resistance to disease' has acquired a more precise significance, and the wide field of research here opened up in this connection promises results of the utmost practical as well as theoretical importance. To the question, 'Who can bring a clean thing out of an unclean?' we are beginning to find an

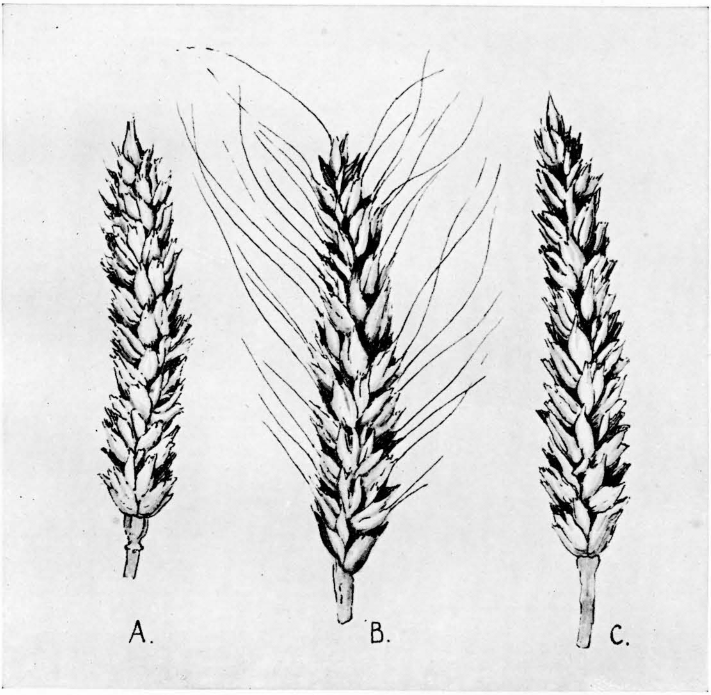

FIG. 39.—Mendelian phenomena in wheat. (After R. H. Biffen.)

A, Stand-up wheat; B, Bearded wheat; C, The hybrid, showing that the beardless condition is dominant over the bearded.

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answer, nor is the answer the same as that once given by Job" (R. C. Punnett, 1905, p. 18).

Silkworms.—Toyama paired Siamese silkmoths, with yellow or with white cocoons; the offspring produced only yellow cocoons. When the hybrids were inbred, the result was two sets, one producing white cocoons, the other producing yellow cocoons, and the proportion was Mendelian—25·037 white and 74·96 yellow. The whites bred true; the yellows when inbred showed themselves to be pure dominants or "yellows" and dominant-recessives—*i.e.* splitting up again into yellows and whites in the usual proportion. More intricate experiments confirmed this general result.

It must be noted, however, that Coutagne has made much more elaborate experiments with different results, which in *many* cases cannot be interpreted on the Mendelian theory. Thus he found (1) that the hybrid forms were sometimes blends of the parents and different from both; (2) that in other cases the brood included some like one parent in a particular character, some like the other parent, and some intermediate; and (3) that in other cases the individuals showed no fusion of characters, but resembled one or other parent. It is likely that the discrepancy may be explained as due to considerable diversity of origin in the domesticated races of silkworm, so that, while they breed true when left to themselves, a disturbance of the usual routine leads to the liberation of latent characters.

Lina lapponica.—Miss McCracken has made a fine study of the hereditary relations in this Californian beetle, which occurs in two types, spotted (dominant) and black (recessive). They are always crossing in natural conditions, but there are no intermediates, and it is easy by isolation to rear a "pure" spotted race and a "pure" black race. When spotted forms are paired they may produce only spotted progeny—a case of extracted dominants. In other cases, however, they yield spotted and black forms (1,021 spotted, 345 black), *i.e.* in the Mendelian proportion of 3 : 1—a case of dominant-recessives inbred.

Snails.—Lang paired "pure" five-banded forms of the common or garden snail, *Helix hortensis*, with bandless forms from bandless colonies. The young of the first generation were all bandless, the banded character being recessive. When these were paired the offspring were bandless and banded in the Mendelian ratio, 3 : 1. Further experiments confirmed this, not only as regards bands, but also as regards colour (yellow or red), size, and the form of the umbilicus. *It may be said, therefore, that common snails* (*Helix hortensis* and *Helix nemoralis*) *illustrate Mendelian inheritance.*

Poultry.—Numerous breeding experiments with poultry have been made by Bateson, Bateson and Punnett, Hurst, Davenport, and others, many of which show Mendelian phenomena with great clearness, while others are strangely conflicting. One of the reasons for the complicated results is evidently to be found in the difficulty of securing thoroughly "pure" breeds, for many that breed true as long as they are inbred tend to liberate latent characters when the ordinary course of breeding is departed from.

Hurst contrasts the following characters, which usually show themselves dominants and recessives; but it has to be admitted that the dominance—always complete for some characters—is for others frequently, or even always incomplete—*i.e.* showing traces of the corresponding recessives.

Dominant Characters.	*Recessive Characters.*
Rose comb.	Leaf comb, single comb.
White plumage.	Black plumage, buff plumage.
Extra toes.	Normal toes.
Feathered shanks.	Bare shanks.
Crested head.	Uncrested head.
Brown eggs.	White eggs.
Broodiness.	Non-broodiness.

Davenport's copiously illustrated work is also of great interest. He shows in case after case that the character dominant in the

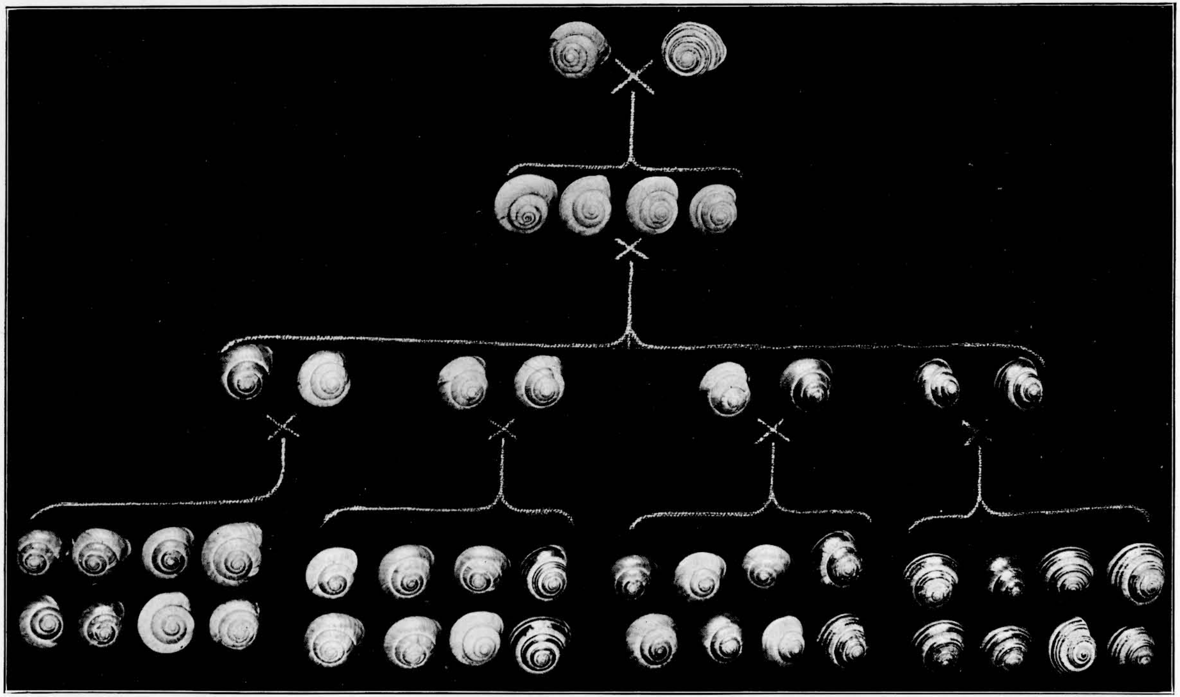

FIG. 40.—Diagram to illustrate Mendelian phenomena in *Helix hortensis*. (After Lang.) The diagram was photographed from random shells, not from the real subjects of experiment, as in Lang's figure.

The first line shows a bandless (D) and a banded (R) form; the bandless form is dominant; the second line shows (F^1) four bandless forms, D(R); the third line shows (F^2) the progeny of the hybrids, 6 bandless and 2 banded 1D+2D(R)+1R; the fourth line (F^3) shows pure extracted bandless dominants to the extreme left, pure extracted banded recessives to the extreme right, in the middle two groups of 3D + 1R.

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first hybrids is more or less influenced by the recessive character. Polish fowls with a large hernia of the brain on the top of the head were paired with Minorcas with normal heads. The hybrids showed no hernia, but most of them showed a frontal prominence. When the hybrids were inbred the hernia occurred in 23·5%—a close approximation to the theoretical 25%.

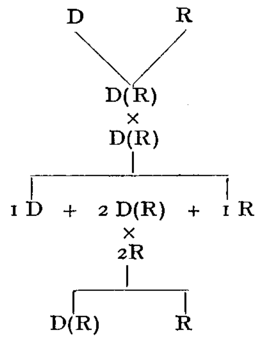
Single-combed black Minorcas were crossed with white-crested black Polish fowls with a very small bifid comb. The hybrids had combs single in front, split behind. When the hybrids were inbred there resulted in a total of 101 offspring, 29·7% with single combs (like Minorcas), 46·5% with Y-shaped combs, and 23·8% with no combs or only papillæ (like the Polish forms). Here, again, the result is in a general way Mendelian, but the Y-like comb is a complication.

Pigeons.—R. Staples-Browne crossed a web-footed pigeon (an occasional discontinuous variation) with a normal form, and got six normal young. In other words, the web-foot character is recessive to the normal foot character. The hybrids were inbred, and in one case produced nine with normal feet and three with webbed-feet—a Mendelian splitting-up. But from another pair of hybrids seventeen normal offspring resulted. Thus, the illustration of Mendelian inheritance is inconclusive. Besides, the numbers were too small.

We have noticed elsewhere that crossing different breeds of pigeons often results in forms which more or less resemble the reputed original ancestor, the wild rock dove; in other words, reversions occur. Often, however, the results seem quite anomalous, which is probably due to the number of latent characters which different races of pigeons appear to carry.

Mice.—Mendelian phenomena have been carefully studied in mice. Thus, when a grey mouse is paired with an albino, the hybrid offspring are always grey. When these are inbred, they yield greys and albinos, approximately in the proportion 3 : 1. Thus Cuénot obtained 198 greys and 72 albinos.

Darbishire has obtained many results which harmonise well with Mendelian theory, while others require some ingenuity if they are to be fitted in with this interpretation. As a good case we may cite one where the inbreeding of pigmented mice—derived from crossing pigmented and albino individuals—yielded 159 pigmented young and 55 albinos (53·5 being the theoretical anticipation). When similar hybrids were paired with pure albinos, they yielded 69 pigmented and 69 albino forms, precisely as the theory would lead us to expect :



Cuénot crossed an albino *A*G (with latent grey) with an albino *A*B (with latent black), and obtained albinos (*A*G*A*B). He crossed a black mouse C*B* with an albino *A*Y (with latent yellow), and obtained yellow mice (CBA*Y*). He then paired *A*G*A*B (albino) with CBA*Y* (yellow) and obtained 151 young—81 albinos, 34 yellow, 20 black, 16 grey ; the theoretical anticipation being—76 albinos, 38 yellow, 19 black, 19 grey. This is an exceedingly striking and convincing case.

Waltzing Mice.—In this well-known breed of fancy mice, only one of the three semicircular canals of the ear attains to development, and this abnormality is associated with the peculiar habit that the animals have of waltzing round in circles. When waltzing mice are crossed with normal mice, their abnormal quality behaves as a recessive.

Rats.—The results reached by breeding rats seem to be more complicated than those obtained in regard to mice. But Bateson's analysis of Crampe's results, and Doncaster's experiments, show that some of the phenomena at least are Mendelian. One of the difficulties, found also in mice, is that the albinos seem often to carry black or brown as a latent character, which crossing may bring into expression.

Rabbits.—Hurst paired white Angora rabbits (with pink eyes and silky hair) with "Belgian hare" rabbits (with pigmented skin, dark eyes, and short yellow fur). The hybrids were pigmented like the "Belgian hares," but the fur was grey like that of the wild rabbit. These hybrids were inbred, and 14 distinct types resulted—an apparent "epidemic of variation" to which Mendel's theory has supplied the clue, for four pairs of contrasted characters are involved in the hybrid inbreeding—namely, short hair versus long hair, pigmented coat versus albinos, grey versus black coat, uniform versus marked coat (Dutch marking latent in the albinos), and the 14 distinct types illustrate the possible combinations.

As regards short hair versus long hair, Hurst found that when the short-coated hybrids were inbred they produced short-haired forms like the Belgian hare grandparent, and long-haired forms like the Angora grandparent. Out of 70 which reached the age of two months or more, 53 were short-haired and 17 long-haired—a close approximation to the Mendelian anticipation, 52·5 : 17·5. Similarly, as regards pigmented coat versus albino, the hybrids, when inbred, yielded 132 pigmented and 39 albino forms—a close approximation to the Mendelian expectation, 129 : 43; and so on.

Cats.—There are some interesting results as to colour (Doncaster). Thus, "pure" orange ♀ crossed by "pure" black ♂ gives tortoiseshell females and yellow males, but black ♀ crossed by orange ♂ gives black males or females, tortoiseshell females, and orange males. It seems that orange usually dominates over black in males, while in females the orange (for some unknown reason) is less dominant and tortoiseshell results. Male tortoiseshell cats are very rare. In this case, the results are complicated by some peculiarity wrapped up with "sex."

When a male tortoiseshell is paired with a female tortoiseshell the kittens are tortoiseshell, orange, and black—which is what Mendelian theory would lead us to expect.

Horses.—In horse-breeding we have usually to deal with a highly prepotent sire, and there seem to be no reliable facts illustrating Mendelian inheritance. It is known, for instance, that bay and brown colours are dominant in relation to chestnut, but this fact is not enough in itself to warrant us in inferring that Mendelian phenomena occur. It has been said by some breeders that in the mating of Clydesdales and Shires there are sometimes Mendelian phenomena.

Sheep.—From statistics published by Graham Bell, illustrations of Mendelian phenomena have been inferred by Davenport. Thus, three white sheep, with exclusively white ancestry (so far as known), were crossed with black sheep, and the 13 lambs were all white. When hybrids of this origin were paired with black sheep, there were 26 white lambs and 25 black lambs—in accordance with the Mendelian expectation. When the hybrid whites were inbred they produced 40 white lambs and 7 black lambs (instead of the theoretical 11 or 12). But the numbers in these cases are far too small to be satisfactory.

When half-bred sheep, resulting from Border Leicester rams and Cheviot ewes, are inbred, they breed *true to their own type*, which is a distinctly non-Mendelian phenomenon.

Man.—There is as yet no secure evidence of Mendelian phenomena in man, but there has not been time for much investigation. Attempts have been made to find evidence in cases of albinism among negroes (Castle) and the lineage of families inclined to polydactylism, but the cases are very inconclusive.*

* Castle's case is reported in *Science*, xvii., 1903, but we have not seen the paper. An albino in a negro family had offspring by a negro, the children were negroes, but in the next generation there was a splitting into negro and albino types.

It would be interesting to have precise information as to the progeny of Eurasians who intermarry, for here the original hybrids result from the mixture of two very distinct races.

Mr. Bateson cites (from Nettleship) a case of congenital cataract which continued to reappear through several generations. He calls the congenital cataract a dominant character, though it was not exhibited in all the F^1 generation ; the normals had only normal offspring ; the affected members had children of both kinds in approximately equal numbers, viz. 29 (?—1) and 26 (+ ?). The pedigree is given elsewhere. Of this and of another pedigree, Bateson says that they " are in good agreement with the Mendelian scheme," but they do not seem to us at all convincing, unless the exception proves the rule.

If Mendelian phenomena occurred in man, it seems unlikely that they should have escaped detection, since crossings of races have been very common. The intermarriage of mulattos should surely have yielded some clear results. There is of course the difficulty that the inbreeding necessary to bring out Mendelian segregation is not sufficiently close in mankind.

It appears to us that something might be made of the fact that there is very frequent marriage, *e.g.* in Britain, between the dark and the fair. This has gone on for centuries, and yet the two types are always with us, and are often strikingly seen in one household. The monotony of an average blended brown has certainly not become general. But this is a complex and difficult inquiry.

§ 5. *Mendel's Discovery in Relation to Other Conclusions*

Conception of the Organism.—A keen critic has pointed out that the Darwinian or Selectionist theory of evolution is obviously a projection on nature of anthropomorphic ideas partly due to the keen competition of the industrial age, partly due to a temporary pressure of over-population, partly due to the process by which mechanical devices, such as spinning and weaving machinery on the one hand and bicycles on the other, are improved by the addition of one patent after another. Taking the last point, the critic asks if we can seriously believe that organisms have evolved by piecemeal variation and selection of particular parts, comparable to improvements now in the gear, again in the steering, and again in the chain of the bicycle? Is it not one of the clearest and surest facts about an organism that it is a unity? It lives as a unity, does it not evolve as a unity?

We cannot here enter into a discussion of the alleged anthropomorphism or sociomorphism of what we flatter ourselves by calling "pure science." That is a very interesting thesis, and worthy of much discussion. But we wish to refer for a moment to the idea of the "piecemeal patenting theory" of evolution, since it seems to us that the *facts* brought to light by Mendel and the Mendelians are sufficient to show that there is some truth in this way of looking at the organism.

It has been shown that some organisms have clear-cut, we may almost say crisp, unit characters, which behave in inheritance as if they were independent constituents, being transmissible *en bloc* and in their entirety—not blending with analogous characters, but remaining quite distinct, and developing in absolute intactness and exclusiveness or not at all.

The Mendelian facts, as Bateson says, lead us to regard the organism as "a complex of characters, of which some at least are dissociable and are capable of being replaced by others. . . . We thus reach the conception of unit characters, which may be rearranged in the formation of the reproductive cells. It is hardly too much to say that the experiments which led to this advance in knowledge are worthy to rank with those that laid the foundation of the atomic laws of chemistry."

Weismann has not paid much attention to Mendel's Law, because he regards the basis of facts as still insufficiently broad, and because he sees so many discrepancies in the experimental results; but it may be pointed out that the general idea of independently heritable unit characters is not inconsistent with, but rather corroborates Weismann's picture of an inheritance as composed of numerous sets of determinants or primary constituents, each corresponding to an independently variable and heritable structure. It is quite possible that the germ-cells of the hybrids of two distinctively contrasted parents do not separate into two sets bearing "pure" dominant determinants and "pure" recessive determinants, but that the practical "purity" is wrought out by a process of germinal selection.

However this may be, the facts of Mendelism lead us to a renewed confidence in the relative independence of unit characters. It looks as if a unit character sometimes behaves like a radicle in chemistry; it can be replaced *en bloc* by another, but it cannot compromise with that other. "The outlook," as Bateson says, "is not very different from that which opened in chemistry when definiteness began to be perceived in the laws of chemical combination."

While the idea of unit characters, which is well backed up by facts, tends to clearness, it must be cautiously worked with.

1. There are only certain peculiarities of the organism of which it can be said that they *demonstrably* behave as unit characters. But this may simply mean that in regard to other peculiarities we have as yet been unable to discover the appropriate contrasted crossing which would bring out the characteristic behaviour of allelomorphs.

2. There are also cases—*e.g.* of inbred crosses of Cheviot and Leicester sheep—where the conception of unit characters remains unverified. It seems to us safer, at present, to say that some but not all the peculiarities of contrasted types behave as "unit characters."

3. Correns points out that what seems at first sight like an independent unit character may turn out to be nothing more than the necessary consequence of another character. "Thus the wrinkled appearance of the sugar-maize seed, in contrast to the

smooth maize seed, is a consequence of its greater content of water in the fresh state, and this again is a consequence of the fact that the seed has dextrin and sugar instead of starch as the reserve material for the embryo. Thereby a difference in weight, in colouring, and in texture is brought about. All these features depend upon a single primordium or rudiment—namely, whether the seed contains dextrin and sugar or starch" (1905, p. 15).

4. The idea of unit characters must be kept in harmony with the indubitable facts of physiological correlation, and the idea of their "independence" must be large enough to include the fact that they seem sometimes to go in inseparable couples.

In many ways, therefore, Weismann's somewhat subtler and more complex conception of determinants which work out a character by co-operative development appears to us to fit the facts better.

A New View of Evolution.—As is well known, Darwin believed that specific differences and adaptations were slowly brought about by the consistent selection of small continuous variations in a profitable direction. He did, indeed, recognise that large discontinuous variations may suddenly arise, as in the case of the short-legged Ancon sheep. He could not, however, lay stress upon such occurrences, believing as he did that they were of rare occurrence, and therefore very liable to be swamped by intercrossing with the normal forms.

Over and over again, both before and after Darwin, naturalists had suggested that sudden emergences of new structures with no small degree of completeness, brusque transitions from one position of organic equilibrium to another, might be of evolutionary importance. We need only mention Etienne Geoffroy Saint-Hilaire and Francis Galton. But the difficulty always was, that these discontinuous variations seemed to be of rare occurrence, and liable to be swamped.

In 1894 Bateson showed in his *Materials for the Study of Variation* that discontinuity in variation was a fairly common phenomenon, and might, therefore, have played in the past an important rôle in the origin of species (see Chapter III.).

Similarly, Hugo de Vries showed in most convincing detail that sudden discontinuous variations or mutations not infrequently occur among plants and give rise to true-breeding varieties (see Chapter III.).

Now it is evident that, if Mendel's Law applies in such cases, the mutation, once present, is not likely to be lost or swamped by inbreeding with the normal types. Thus, through Mendel's discovery we are led to a new view of organic evolution, in which we attach less importance to the minute fluctuations on which Darwin relied, and more importance to mutations or saltatory variations.

Mendelism in Relation to Selection.—The facts of Mendelism are in several ways important in relation to natural selection:—(1) The facts warrant us in believing in the possibility of the particular evolution of unit characters while the rest of the organism remains stable. (2) When a variation is, through inherent stability or through inbreeding, prepotent—*i.e.* when its possessors breed true *inter se*—we can understand how it is that even crossing with variants having an antagonistic character need not imply any diminution of the dominance of the character in question. The inbreeding of the hybrids simply results in the sifting out of the pure parental types. (3) Suppose Mendelian phenomena to occur in a series of generations, and suppose that natural selection favours the possessor of the dominant character, they will *ex hypothesi* prevail as elimination proceeds. But it should also be noted that, apart from selection, the possessors of the dominant character will be in a gradually increasing majority, since extracted dominants and dominant-recessives (practically indistinguishable as far as natural selection goes) are always to recessives in the proportion of 3 : 1.

In the beautiful case of the two nettles given by Correns, the plants with entire leaf-margins are markedly more susceptible to fungoid attacks than those with dentate margins, so that in the course of time in certain conditions the former race would tend to be eliminated by natural selection ; but it is also handicapped by the hereditary conditions, since three dominants are always being produced to one recessive.

Swamping Effects of Intercrossing.—A well-known objection to Darwinism, first clearly stated by Prof. Fleeming Jenkin, is that variations of small amount and sparse occurrence would tend to be swamped by intercrossing before they had time to accumulate and gain stability. In artificial selection the breeder takes measures to prevent this "swamping-out," by deliberately pairing similar or suitable forms together, or by deliberately removing undesirable forms ; but what, in nature, corresponds to the breeder ?

Various answers are possible:—(1) It may be that similar variations occur in many individuals at once and many times over. (2) It may be that the variations which really count in evolution are not small individual fluctuations, but discon*tinuous variations. (3) It may be that many variations* are not from the first unstable, but express changes of organic equilibrium which come to stay if they get a chance at all. (4) There are numerous conditions in nature—summed up in the concept "isolation"—*e.g.* geographical barriers, differences in habit, psychical likes and dislikes—which tend to prevent free intercrossing between sections of a species. Similar forms may pair, and, in various ways, assortative mating may come about naturally. And whenever inbreeding sets in prepotency develops—*i.e.* peculiarities, even if trivial, gain great staying-power in inheritance. (5) But even more important are the facts disclosed by Mendel and his school, that crossing does *not* tend to swamp new features, for if the hybrids be inbred there is a persistent segregation of the parental type. A new mutant crossed with a related form of contrasted character may be dominant or recessive in the immediate hybrid (F^1), but in either case, if the hybrids are inbred, it will reappear in pure form in the next generation (F^2), and so forth. There is, however, no warrant for the common belief that hybridisation in itself gives rise to new races.

Mendelism and Weismannism.—Mendel's discoveries lead us to regard the inheritance as built up of "items," which may be inherited independently—*e.g.* unit characters corresponding to the "unit characters" of the organism, tallness, dwarfness, yellow albumen, green albumen, purple colour of flowers, white colour of flowers, and so on. These correspond to Weismann's primary constituents or determinants—the germinal representatives of the independently heritable and independently variable characters of the organism.

In crossing grey and albino rabbits, Mr. C. C. Hurst obtained in the F^2 families, cases of three grey : one albino ; and cases of nine grey : three black : four albino ; in either case, according to the Mendelian rule, three coloured : one albino.

"The albinos can give no more coloured. The blacks may be pure blacks, or they may give blacks and albinos. The greys may be pure greys ; or they may give greys and albinos ; or greys and blacks ; or greys, blacks, and albinos, as before.

"Of the four albinos, for instance, which appear on an average in 16 F^2, one will be carrying the grey determiner, one the black determiner, and two will have both grey and black determiners. By suitable cross-matings the condition of each albino can be exactly determined. For example, when bred to a pure black, a G albino will give greys only ; a G B albino will give equal numbers of greys and blacks ; while a B albino will give blacks only. Similarly, the exact composition of each coloured rabbit may be determined by experimental breeding.

"The particular colour of a rabbit or mouse is therefore not a simple character depending on the presence of a single factor, but a double one, depending on interaction between one factor and another, each factor being transmitted independently in heredity."

It seems to us that these complexities land us in close approximation to the concept of germinal selection.

Mendelism in Relation to Ancestral Inheritance.—It may be that the conception of ancestral inheritance and the conception of segregate parental inheritance apply to different sets of cases.

1. At one extreme we may perhaps place cases of sterility, where the fertilised egg-cell fails to develop, owing perhaps to mutual incompatibility between the paternal and maternal contributions. "The sterility of distinct species when crossed is probably due to the confusion and disruption of the systems of forces in the pronuclei of the germ-cells by antagonising ancestral stimuli" (Dendy, 1903).

2. It is *possible* that in some cases where a spermatozoon enters an egg it fulfils one of its functions—acting as a liberating stimulus prompting the egg to develop—and yet does not fulfil its other function of contributing half of the inheritance. It is *possible* that it is sometimes only the egg-nucleus which develops. This possibility is suggested by some of the results of experimental embryology—*e.g.* that an egg may develop with only a sperm-nucleus (merogony), or with only its own nucleus (artificial parthenogenesis).

3. Dendy suggests that those remarkable abnormal insects (see Darwin, *Variation of Animals and Plants under Domestication*, vol. ii. p. 394), in which one-half or one-quarter of the body is like that of the male and the other half or three-quarters like that of the female, may be due to an inadequate blending of the male and female nuclei. "They may separate completely at the first or at some subsequent division of the segmentation nucleus, and thereafter each may control a certain fraction of the developing organism, yielding a lop-sided result."

4. The maternal and paternal contributions may remain together in the development of the body, though one is dominant, but they may be dissociated in the formation of the germ cells, so that two sets of germ-cells result (Mendelian inheritance).

5. The maternal and paternal contributions may find equal

expression in development, and through them ancestral contributions may also find realisation (Galtonian inheritance).

There should not, of course, be any opposition between Mendelian and Galtonian formulae, for that is a confusion of thought, to obviate which we have sharply separated the statistical from the experimental study of inheritance. They are correlated, and ultimately they will be seen in complete harmony, as different aspects of the same phenomena. But it is simply muddle-headedness which can find any opposition between a statistical formula applicable to averages of successive generations breeding freely, and a physiological formula applicable to particular sets of cases where parents with contrasted dominant and recessive characters are crossed and their hybrid offspring are inbred. We may refer to the admirable essay by Darbishire (1906).

§ 6. *Practical Importance of Mendel's Discovery*

As Mendel's discovery is extended it is bound to have a great influence on the breeding of animals and the cultivation of plants. Wherever it is applicable it will afford a solid basis for action, enabling the breeder to reach his desired result more surely, more rapidly, and more economically. The case we have mentioned of the varieties of wheat susceptible and immune to "rust" is in itself very suggestive.

Possible Application to Mankind.—Although we do not yet know of any reliable illustration of Mendelism in reference to man, and although it does not apply in the familiar case of mulattos, it would be rash to conclude that there is no application. Search must be made for cases where two parents of well-marked prepotent stocks differ from one another in sharply defined unit characters. It must be remembered that intermarriages between very different stocks are still common, and that crossing of different races has been frequent in the past.

When we think of Mendel's discovery in relation to our own race, to which it may *possibly* apply, we see that its main idea enormously enhances the importance of the hereditary factor in determining evolution; for it leads us to realise more strongly the power of persistence that definite characters may have even when there is intercrossing. Definite characters for good or ill, whether dominant or recessive, do not disappear in Mendelian inheritance. They persistently reappear in their original "purity."

Thus, Mr. Punnett writes: "Permanent progress is a question of breeding rather than of pedagogics; a matter of gametes, not of training. As our knowledge of heredity clears and the mists of superstition are dispelled, there grows upon us with an ever-increasing and relentless force the conviction that the creature is not made, but born" (1905, p. 60).

Inbreeding.—Breeders who have with carefulness evolved a fine herd are often very loath to introduce fresh blood, even when they suspect that they are approaching the limits of safe inbreeding. But *if* Mendelism applies to the organisms bred, then it does not seem as if the introduction of fresh blood need affect the purity of the stock. A cross is effected with a view to secure reinvigoration; the results of the cross may be inbred, and *if Mendelism applies*, then forms like the original parent will reappear in the next generation, and the forms not wanted can be disposed of. Let us put it once more in schematic form:

Old-established form. "Fresh blood."
A B

If A be dominant, A(B); or B(A), if B be dominant.
× ×
A A

n A + n A(B) n A + n B(A)

Or if A(B) be inbred the result will be n A + 2 n A(B) + n B.
Or if B(A) be inbred the result will be n A + 2 n B(A) + n B.
There is obviously no *theoretical* danger of losing A.

No one can, of course, at present say that these "simple equations" will apply to the introduction of fresh blood into a herd of cattle, but the time has come for more daring experiment on Mendelian lines. It might obviously happen that the "fresh blood" (B) introduced was quite incompatible with the pure-bred (A), and the progeny was an undesirable freak. But do not such casualties happen under the present instinctive or empirical régime followed by most breeders?

A few Illustrations from Stock-breeding.—As everyone knows, elaborate experiments on heredity have been carried on for many years by breeders of horses and cattle, and increased effort should be made to tap their valuable records. We cannot attempt this here, but we give two or three illustrations, kindly placed at our disposal by Mr. John Marr of Uppermill, Tarves, and Mr. Duthie of Collynie, two well-known breeders. As the facts were partly stated in conversation, we must bear the responsibility of any inaccuracies.

In answer to a question regarding the general origin of famous breeds of cattle, Mr. Marr's statement is briefly as follows: "As to the historical origin of recent breeds of cattle, it seems to be generally true that men like Cruickshank, Booth, Bates, Collings, and McCombie began with a more or less random selection of good specimens of the ordinary stock of the country. A good pedigree was at first simply a pedigree built up of good individual ancestors. The second step was to strengthen the herd by elimination and to fix excellence by inbreeding and selective breeding. In most cases, however, there seems to have been a critical moment in the history of the herd when a particularly good sire turned up, such as Champion of England in the history of the Cruickshank Shorthorns. The breeders then used the dominant sire and his male progeny on the different families of cows composing the herd, until his most excellent blood seemed to permeate the whole. Finally, there seems to arise a limit of profitable inbreeding, when new blood has to be introduced. The first bad effect of inbreeding is some loss of size in successive generations. Afterwards come impaired constitution and fertility." If the breeder introduces a strongly inbred sire of a different line there is conflict between the two powerful strains. "The type is apt to be destroyed and the progeny sports in many directions. Probably the safest course is to use a sire of rather mixed blood, and then the chances are that the concentrated female blood will continue to rule the type of the progeny, and a substantial gain in vigour and fertility will be secured."

The following case, due to Mr. Marr, is of some interest. Two Clydesdale stallions, full brothers, were of very different type. One was of the pure Clydesdale type, and was very prepotent in breeding true to that type. The other was nearly of the Clydesdale type, but with a trace of the Shire in his appearance, and he was a very prepotent getter of stock more like the Shire than himself. The sire of these stallions was a very pure Clydesdale, the dam had a small admixture of Shire blood. There was here, perhaps, the beginning of a sifting out of the Shire character.

As is well known, the Shorthorn, the Hereford, and the Aberdeen Angus are the three leading breeds of beef cattle, each very prepotent according to its kind. Mr. Marr relates a remarkable instance of the result of crossing these three breeds, which came under his personal observation. A cross bull, whose sire was a pure Hereford bull and whose dam was a Shorthorn-cross cow, was mated with a pure black polled Aberdeen Angus cow. The colour of the Shorthorn-cross cow is a little uncertain, but it is believed to have been red with a little white. The colour of the cross bull was red with white face and hind legs. In any case there was an interesting mixture of breeds, and the produce was a beautiful creamy white heifer, with black muzzle and black hair on the inside and tips of the ears. She had a very stylish head and horns, and bore a striking resemblance to Chillingham white cattle. Other nine calves bred on similar lines showed no special points of interest, except that they differed very much from one another. It is possible that the creamy white colour was a reversion to an ancestral type, such as the Chillingham cattle may represent. It seems more likely that a white bull had figured at no remote period, *e.g.* in the lineage of the Shorthorn, for white bulls are often used to secure the desired roan colour. It is generally admitted that when there is an occurrence of white colour, either on the body generally or in markings on the face and legs, it is difficult to breed out, often reappearing with extraordinary persistency. The pedigree referred to is as follows :—

- Horned creamy white heifer .
  - Sire. Red cross horned bull, with white markings .
    - Sire. Pure Hereford bull, red with white face and hind legs.
    - Dam. Shorthorn-cross cow, (roan or) red with some white markings, horned . .
      - Sire. Pure Shorthorn bull.
      - Dam. Shorthorn-cross cow.
  - Dam. Pure black polled Aberdeen Angus cow.

The following instance may illustrate that, in spite of the popular impression to the contrary, the breeders cannot always have their own way. Variation leads and the breeders follow, not conversely. In Shorthorn cattle the standard colours are red, red-and-white, roan (a close mixture of red and white hairs) and white. The popular colours are red and roan, and breeders try to avoid white, and red-and-white. But these unpopular colours are continually occurring. "If a roan cow is mated with a roan bull year after year and produces several roan or red calves, there is an increasing chance every year that she will produce a calf of one of the unpopular colours." Similarly red cow and red bull may have the unpopular red-and-white calves.

Mr. Duthie of Collynie has told us of the following case :—

A light roan cow of very good quality was served repeatedly by a crack light roan bull. She had three or four very good white calves. But a roan calf was much desired, and the following experiment was tried. She was served by the roan bull, and at the same time she had in view—over the wall—a red yearling, which was afterwards put into the next stall. The cow eventually gave birth to a red roan heifer calf of great beauty. This is not an isolated case. From a pure white bull and a white cow a fine red roan calf was produced, and this was attributed to the fact that the white cow was continually accompanied by a red cow !

It often happens that the crossing of a white bull and a red cow yields a roan, and it sometimes happens that when this roan is served by a roan bull, the result is a white calf. If this sort of experiment were followed up, it might be found that Mendelian phenomena occur.

§ 7. *Other Experiments on Heredity*

Our survey of cases must be supplemented by reference to the works of Bateson, T. H. Morgan, De Vries, and others ; but we have said enough to show,—(1) that Mendelian phenomena are well illustrated in certain cases—*e.g.* peas, mice, rabbits, poultry, snails ; (2) that in other cases, while there are clear Mendelian phenomena according to some observers, discrepant results have been reached by others—*e.g.* silkmoths ; (3) that in other cases, while there are hints of Mendelian phenomena, the results cannot be interpreted in conformity with Mendelism without far-fetched ingenuity—*e.g.* pigeons ; and (4) that in other cases the results of hybridising do not at all agree with Mendel's Law—*e.g.* in sheep and man.

It seems to us that the results depend in part on whether there are or are not sufficiently well-marked contrasted unit characters in the two parents. When the differences between the two original parent-types are not crisply definable in terms of contrasted unit characters, the conditions of Mendelian inheritance are not afforded, and we have to fall back upon the old-fashioned description of the inheritance as "blended" or "particulate" or "reversionary," and so forth.

It must be clearly noted that Mendelian phenomena are not known except in certain cases of hybridisation. They chiefly occur in the inbreeding of the hybrid progeny of two well-marked varieties or "elementary species." We do not know how far they may be found to apply in the breeding of pure strains.

Karl Pearson's studies on the inheritance of coat-colour in horses and dogs and of eye-colour in man are as far as possible from suggesting that Mendelian inheritance is illustrated in these cases. It appears that the colour of coat or of eyes in the offspring is a function of the ancestral rather than of the parental characters. Yet, it is quite conceivable that Mendelian inheritance may be demonstrated in horses, dogs, and man—in cases where the parents do not contain a medley of latent strains, but are sharply contrasted with one another in respect to one or more unit characters. The danger is of trying to universalise the Mendelian formula, and some of the attempts that have been made to give a Mendelian interpretation to discrepant facts seem to us very far-fetched.

There is, we think, much reason to believe that in some cases the unit characters are represented in the germ-plasm by determinants which are very stable in themselves, which must be everything or nothing in the hypothetical struggle antecedent to and associated with development, whose expression will not blend with, or even allow of the expression of contrasted analogous determinants. There is, we think, equal reason to believe that in other cases the unit-characters are not so "exclusive," but may combine with analogous unit characters to form a blend or a particulate mosaic.

Non-Mendelian Results.—In a lecture on Heredity which the late Professor Weldon delivered in 1905, an account was given of some of Tschermak's experiments on peas and beans, the results of which do not harmonise well with the Mendelian formula. (See *The Lancet*, March 25, 1905, p. 810.)

Tschermak crossed two races of peas characterised by cotyledons of two different types of growth,—epigeal and hypogeal. The hybrid progeny of the crossing showed 30 plants with epigeal cotyledons, 32 with the hypogeal habit, and 18 of intermediate type—obviously "a very imperfect segregation." In the third generation none of these bred true; each produced, when fertilised by its own kind, a mixed progeny of all the three sorts.

Tschermak crossed a white-flowered pea (*Pisum sativum*) with a red or purple species (*Pisum arvense*); the hybrid progeny resembled the latter; the red colour was dominant. But when these were fertilised from their kind, they yielded out of 397 plants, 239 red, 75 rose, and 83 white—a proportion of 9 red, 3 rose, and 4 white, which cannot be called Mendelian. Tschermak suggested, however, that if white and rose were postulated as the ancestral colours of the two races of peas, the results would more closely conform to the Mendelian formula.

Tschermak went on to work with the red (239), rose (75) and white (83) plants, fertilising each type from its own kind, and he found that of the reds some produced red and others white and rose-coloured offspring, that of the whites the offspring were mostly white, while most of the rose-coloured plants yielded only a rose-and-white progeny. This, again, does not seem to be a Mendelian result.

Tschermak also crossed bronze and white kidney beans, and got a hybrid progeny with seed-coats of a dark brown colour mottled with black spots and "tortoiseshell" markings (488 seeds) and with white seeds (161). The mottled seeds when sown gave rise to "coloured" and white-seeded beans. Of the coloured seeds 52 per cent. were of the mottled "tortoiseshell" appearance and 48 per cent. were of a uniform bronze colour. This, again, is not a Mendelian result. The white seeds bred true, and in the fourth generation all the mottled seeds bred true,—the mottling having become apparently a dominant character.

There seems at present no reason to believe that the Mendelian formula has more than a limited application, though it is of course possible that apparent exceptions may eventually turn out to be less formidable than they seem. There seems no reason why there should not be several formulæ of inheritance—each applicable to particular sets of cases, *e.g.* to cases where blending does occur and to cases where it never occurs. As the method of experiment is obviously the surest line of progress, the more it is prosecuted the sooner will the mists surrounding heredity disappear, but progress cannot be secured by ignoring difficult cases or by straining the formula in the eager desire to universalise it.

Johannsen's Experiments on "Pure Lines."—Prof. Johannsen of Copenhagen has made experiments on the inheritance of quantitative characters, *e.g.* weight of seeds, in "pure lines" of barley, beans, and other plants. By a "pure line" he means all the descendants of a single plant, the mode of reproduction being by self-fertilisation. The members of such a pure line showed "normal variability" in the weights of their seeds, that is the variations in the weights, when plotted out, gave the normal curve of frequency.

Selecting a markedly divergent member of a particular pure line, Johannsen bred from it, and found that its offspring showed regression to the mean of the line from which it had been selected, but not to the mean of the general population of beans. It seems as if the inbreeding established a kind of sub-stock to the mean of which the offspring of divergent members showed a tendency to approximate, but this mean is different from that of the general population. In other words, selection of quantitative characters within a "pure line" is not effective like selection in a population.

Blended Inheritance.—The progeny of a white and a black is a mulatto, and mulattos intermarrying breed true, neither white nor black reappearing. It is a clear case of blended inheritance, and of blended inheritance remaining stable. And this applies to the hair as well as to colour. When mulatto marries white, there is again a blend. When mulatto marries black, there is again a blend. There is not the least hint of Mendelian inheritance. Similarly in quite a number of hybridisations—*e.g.* dog and jackal, horse and ass, lion and tiger, brown bear and polar bear—there is blending, though one parent may be more or less prepotent.

Half-bred Sheep.—An experienced breeder, Mr. John Marr of Uppermill, Tarves, Aberdeenshire, has expressed to me his conviction that the Mendelian formula does not apply, for instance, to the case of half-bred sheep.

"Border Leicester rams mated with Cheviot ewes produce half-bred lambs, and these when mated with each other continue in successive generations to breed true to their own type with very little (if any ?) tendency towards either of the parent breeds."

Particulate Inheritance.—There is no doubt that in some cases the offspring of two more or less different parents may show the characters of one parent in one part of the body and the characters of another parent in another part of the body,—*i.e.* particulate inheritance—*e.g.* in piebald horses, cattle, dogs, etc. A cross between a red and a white flower may be a white flower with red stripes or *vice versâ*. Correns refers to the popular impression that this mode of inheritance is very common and says that this is very far from being the case. Where hybridising normally yields this mosaic-like result, it usually turns out that the mosaic pattern was really in one or both of the parents, though it may have remained quite latent.

Exclusive Inheritance.—When two more or less different forms are crossed it often happens that the offspring resemble one parent exclusively. The characters of the other parent remain latent. This resembles the first stage in Mendelian inheritance, where the *dominant* characters alone find expression. In old-fashioned phraseology one parent is thoroughly prepotent. But if the hybrids breed true when paired *inter se*, or if they produce forms like only one of the grandparents, or if they produce a reversion to an ancestral type, or if they produce something quite novel, then we are not dealing with Mendelian phenomena.

Hybridisation in General.—It is not desirable to attempt to draw any definite line between the various kinds of crossings—which may all be arranged on an inclined plane—for they differ simply in the degree of difference between the two parents. We may conveniently use the word "hybridisation" (cross-breeding, outbreeding, exogamy) whenever there is a marked difference between the two parents. The cases may be arranged on an inclined plane.

.. .. Different genera.
.. .. Different species.
.. .. Different subspecies.
.. .. Different breeds.
.. .. Mutants.
.. .. Variants.
.. .. Apparently identical forms.
.. .. Self-fertilisation (autogamy).
.. .. Parthenogenesis.

Examples.—Individuals belonging to different *genera—e.g.* domestic fowl and pheasant, sea-urchins, different genera of orchids.

Individuals belonging to different *species—e.g.* capercaillie and black grouse, carrion crow and hooded crow, different species of *Saturnia*, different species of *Medicago*.

Individuals belonging to different subspecies—*e.g.* maize.

Individuals belonging to different breeds—*e.g.* poultry, short-horn and Aberdeenshire Angus cattle, Clydesdale and Shire horses, silkmoths.

Individuals belonging to different "varieties" which have not risen to the stability of "breeds"—*e.g.* wheat susceptible and immune to rust.

Hybridisation of Distinct Species.—The conception of species is confessedly quite relative—it is *a term of convenience* when we wish to include under one title all the members of a group of individuals who resemble one another in certain characteristics. A species is often simply a segment of a curve of closely related forms. It is a statistical conception, and as there is no absolute constancy in specific characters, as one species melts into another, with which it is connected by intermediate varieties, by frequent or casual variations, we have to confess that it is a human device, the validity of which varies greatly according to our knowledge or ignorance of the forms in question. A specific name is sometimes, when we are very ignorant, as unmeaning as the name of a constellation in the starry heavens. But it is equally convenient.

At the same time, since science is systematised common sense, it is usually admitted—oftener, perhaps, as a pious opinion, than as a practice—that the characters on account of which a naturalist gives a specific name to a group of similar individuals *should be more marked than those which distinguish the members of any one family, should show a relative constancy from generation to generation, and should be associated with reproductive peculiarities which tend to restrict the range of mutual fertility to the members of the proposed species* (see the author's *Outlines of Zoology*, 4th ed., 1906, pp. 14-16).

The popular impression that crosses between "distinct species" are rare is erroneous; for, apart from the familiar mules, fertile pairing is known between lion and tiger, dog and jackal, wild and domestic cat, brown bear and polar bear, American bison and European wild ox, horse and zebra, hare and rabbit, duck and goose, canary and finch, thrush and blackbird, capercaillie and blackcock, carrion crow and hooded crow, pheasant and fowl, and the list soon becomes very long if we include backboneless animals and plants (see *Evolution of Sex*, revised ed., 1901, p. 163).

The popular impression that fertile crosses between "distinct species" result invariably in sterile offspring is also erroneous; for the hybrids of American bison and European wild ox, of Indian humped cattle and domesticated ox, of common goose and Chinese goose, of common duck and pintail duck, of different kinds of pheasants, and many more are certainly fertile.

At the same time, the general statement may be safely made that successful crossing and the fertility of the hybrid offspring is in inverse proportion to the distinctness of the species crossed.

It seems also safe to say that the characters of species-hybrids do not conform to any general formula. They may be a blend of the parental characters, they may be exclusive or particulate, they may be reversionary—*i.e.* allowing expression of long-latent ancestral characters—or they may be novel and peculiar.

On the whole, the crossing of distinct species, while it may be interesting physiologically, does not seem to have much interest for the evolutionist. It does now and then occur in nature, but it seems to be a mere by-play of little phylogenetic importance—unless perhaps in very early days, of which we know nothing.

Diverse Results of Hybridising.—An inheritance is such a complex integrate of items that no one can hope to predict the result of mingling two more or less distinct inheritances. We have two organisms, A and B, which can be crossed and produce offspring: but, before the germ-cells of A and B are ready for union, they have undergone a process of maturation which may definitely affect the burden of hereditary qualities of which each germ-cell is the vehicle; by the process of amphimixis or fertilisation a new integrate or zygote is formed—the fertilised egg-cell—and in this integration the inheritance may be affected by permutations and combinations, mutual adjustments and new states of equilibrium, victories and defeats of particular items, of all which we have no actual knowledge. In he process of development, if there are several different sets of primary constituents representative of a future structure—an hypothesis from which we can see no escape—then the result may in part depend on the struggles and interactions of these in the course of development; for, as we have often said, it does not follow that everything represented in the inheritance finds expression in development. Finally, it must be remembered that the process of development implies interaction between the inheritance and an appropriate environment, and that since this appropriate environment is variable (within limits of the embryo's viability) the result may again be *modified* by minor peculiarities of nurture. It is, therefore, plain that prediction as to *individual* results of crossing is out of the question.

The Mendelian theory has thrown light on the variability which has often been remarked when crosses have been effected. Cross-breds are produced and inbred, and new forms appear in their progeny. The Mendelians contend, in Mr. Bateson's words, that "in all the cases which have been properly examined these *new* forms are created by simple re-combination of characters brought in by the original parents."

Mr. Bateson gives the instance of crossing a red variety of some plant, say a stock, with a cream-coloured variety. The red variety is characterised by red sap with colourless corpuscles, the cream variety by yellow corpuscles in colourless sap. The red is dominant (F^1). But in the next generation (F^2), we have 9 red, 3 red with cream, 3 *white*, and one cream. What is the meaning of this white, with colourless corpuscles in colourless sap ?

Parents	Red variety × Cream variety			
Allelomorphs or contrasted-unit characters	Red sap (D) Colourless corpuscles (D)	Colourless sap (R) Yellow corpuscles (R)		
F^1	Red sap and Colourless corpuscles			
F^2	Red sap Colourless corpuscles	Red sap Yellow corpuscles	Colourless sap Colourless corpuscles	Colourless sap Yellow corpuscles
Appearance	9 Red	3 Red-Cream	3 White	1 Cream.

"Which are the factors which segregate in the formation of the germ-cells ? They are (*a*) red sap from colourless sap, and (*b*) white corpuscles from yellow corpuscles ; so that when the possible combinations of these two pairs of characters are made, colourless corpuscles may coincide with colourless sap and a white flower is the result" (Bateson, 1906).

SUMMARY.—There are several well-known results of hybridisation :

1. The hybrids may be an intermediate blend of the parental characters, as in mulattos, finch and canary, carrion crow and hooded crow, and in many plants,—

$$A \times B \text{ yields } \frac{AB}{2}$$

2. The hybrids may show a particulate juxtaposition without a blend of the parental characters, as in piebald animals, or in cross between male Lady Amherst pheasant and female golden pheasant,—

$$A \times B \text{ yields } \frac{A + B}{2}$$

3. The hybrids may resemble an ancestral form, whose characters have not been recently patent, as in many crossings of pigeons, red-eyed albino house-mouse and Japanese waltzing mouse (with progeny like wild

mouse), white Angora rabbit and Belgian hare rabbit (with progeny like wild rabbit),—

A × B yields *r* (AB)

4. The hybrids may be quite different from either parent, "with a character of their own"—*e.g.* Andalusian fowl,—

A × B yields C

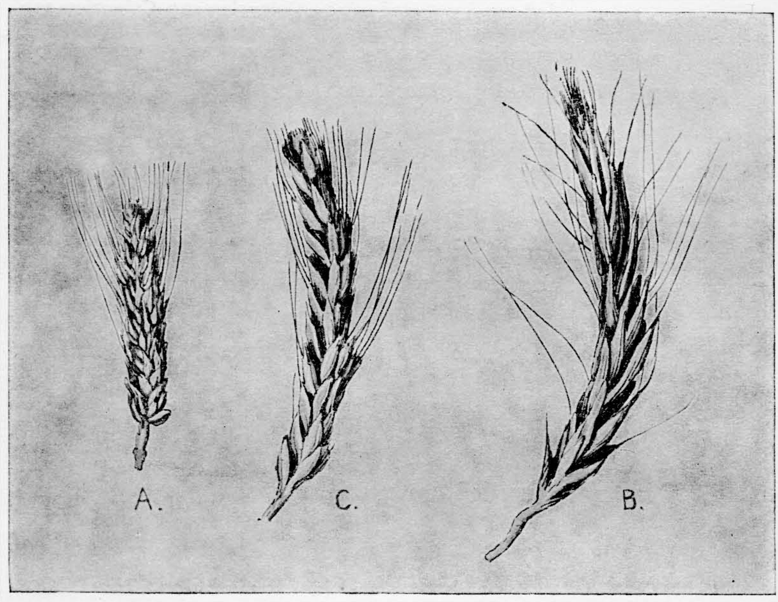


FIG. 41.—Varieties of Wheat. (After R. H. Biffen.)

A, Rivet; B, Polish; C, The hybrid Rivet × Polish, intermediate in laxness and glume length between its parents.

5. The hybrids may exhibit the (dominant) characters of one parent, the (recessive) characters of the other parent remaining latent; this is the first step in Mendelian inheritance,—

A × B yields A(B)

It has been stated in some cases,—(1) that the hybrid shows more of the character of that parent which is phyletically older or more securely established—see *e.g.* some of the results of Standfuss; (*b*) that the hybrid shows more of the character of that parent whose gametes were relatively more mature at the time of fertilisation—*e.g.* some of the results of Vernon. Other generalisations have been ventured, but all require to be revised in the light of what we now know of Mendelian phenomena.

Sometimes, as in mules, the hybrid offspring are sterile. This may show itself (1) in atrophy of the reproductive organs, (2) in abnormalities in the reproductive ducts; or (3) in more obscure conditions in regard to which we can only shroud our ignorance with the words, "constitutional incapacity."

§ 8. *Consanguinity*

Consanguinity.—In many peoples—Jewish and Mohammedan, Indian and Roman—laws against the marriage of near kin go back to remote antiquity, but it seems probable that the basis of these was social rather than biological. In other peoples—Persian, Phœnician, Arab, and even Greek—consanguineous marriages were permitted and sometimes encouraged. The idea that the marriage of near kin is a cause of degeneracy seems to be relatively modern, and is probably based in large measure on the observed degeneracy in closely intermarried noble families. In certain closely inbred communities, moreover, a large percentage of deaf-mutes and weak-minded has been often observed. But it is not difficult to find counter-instances—*e.g.* in the Norfolk Islanders and in the people of Batz on the lower Loire—where close inbreeding has *not* been followed by ill-effects. Mr. George H. Darwin has made out a strong case in support of the position that consanguineous marriages are not in themselves causes of degeneration or of diminished fertility.

Biologically it seems certain that close inbreeding can go far without affecting physique, and that it is very useful in fixing character and developing prepotency. It seems equally certain that, if there be any morbid idiosyncrasy, close inbreeding likewise tends to perpetuate and augment this. The same is doubtless true in the case of mankind, though here the problem is complicated by social considerations which may be just as important as those of bodily health. But the idea that there can be any objection to the marriage of two healthy cousins who happen to fall in love with one another is preposterous.

Darwin's Conclusions.—Charles Darwin devoted much attention to the question of inbreeding (see especially his *Animals and Plants under Domestication*), and his conclusions were: (1) "The consequences of close interbreeding carried on for too long a time are, as is generally believed, loss of size, constitutional vigour, and fertility, sometimes accompanied by a tendency to malformation"; (2) "The evil effects from close interbreeding are difficult to detect, for they accumulate slowly and differ much in degree in different species, whilst the good effects which almost invariably follow a cross are from the first manifest"; (3) "It should however, be clearly understood that the advantage of close interbreeding, as far as the retention of character is concerned, is indisputable, and often outweighs the evil of a slight loss of constitutional vigour."

Experiments.—Weismann inbred mice for twenty-nine generations, and his assistant Von Guaita continued the inbreeding for seven more generations. The general result was a notable reduction of fertility—about 30%.

Ritzema-Bos inbred rats for thirty generations; for the first four years (twenty generations) there was almost no reduction of fertility, but in the following generations there was very marked decrease of fertility, increase of mortality, and decrease of size. But there was no disease or abnormality, such as other experimenters—*e.g.* Crampe—have observed. It goes without saying that if there is a diseased stock, or rather a stock with an hereditary predisposition to disease to start with, then the evil results of inbreeding will soon be evident. But the point is, what will happen if the stock be healthy?

Extensive experiments by Castle and others on the inbreeding of the pomace-fly, *Drosophila ampelophila*, led to the general result that "inbreeding probably reduces very slightly the productiveness of *Drosophila*, but the productiveness may be fully maintained under constant inbreeding (brother and sister) if selection be made from the more productive families."

It seems well established that some stable and important breeds of cattle—*e.g.* polled Angus—have arisen under conditions involving in the early stages extremely close inbreeding, and it is well known in horse-breeding that very valuable results have been reached by using the same stallion repeatedly on successive generations.

Thus, if we take the pedigree of the short-horn bull "Courtier," calved January 6th, 1896, owned by the Iowa Agricultural College, we find from the tabulation given by Mr. R. W. Barclay that "Champion of England" (17526) appears in the pedigree over twenty-five times, and "on both sides of the house." We find another famous bull, "Roan Gauntlet" (45276), functioning over and over again in the lineage. Let us take, for instance, the pedigree of the paternal grandfather of "Courtier" (See p. 394).

- Courtier
  - Prince Bishop
    - Dunblane
      - Roan Gauntlet
        - Royal Duke of Gloster
          - Grand Duke of Gloster
            - Champion of England
            - Duchess of Gloster 9th
          - Mimulus
            - Champion of England
            - *Mistletoe*
        - Princess Royal
          - Champion of England
            - Lancaster Comet
            - Virtue
          - Carmine
            - The Czar
            - Cressida
      - Duchess of Gloster 21st
        - Barmpton Prince
          - Viceroy
            - Champion of England
            - Violet's Forth
          - Butterfly's Delight
            - Allan
            - Butterfly's Joy
        - Duchess of Gloster 13th
          - Grand Duke of Gloster
            - Champion of England
            - Duchess of Gloster 9th
          - Duchess of Gloster 12th
            - Champion of England
            - Duchess of Gloster 7th
    - Duchess of Gloster 24th
  - Sweet Charity 4th. In the dam's *lineage* we find, just as above, Barmpton Prince, Princess Royal, Roan Gauntlet, Royal Duke of Gloster, *Viceroy*, *Butterfly's* Delight, and Champion of England.