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MENDEL'S LAW OF HEREDITY.

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What will doubtless rank as one of the great discoveries in biology, and in the study of heredity perhaps the greatest, was made by Gregor Mendel, an Austrian monk, in the garden of his cloister, some forty years ago. The discovery was announced in the proceedings of a fairly well-known scientific society, but seems to have attracted little attention and to have been soon forgotten. The Darwinian theory then occupied the centre of the scientific stage and Mendel's brilliant discovery was all but unnoticed for a third of a century. Meanwhile the discussion aroused by Weismann's germ-plasm theory, in particular the idea of the non-inheritance of acquired characters, had put the scientific public into a more receptive frame of mind. Mendel's law was rediscovered independently by three different botanists engaged in the study of plant-hybrids, — de Vries, Correns, and Tschermak, — in the year 1900. It remained, however, for Bateson, two years later, to point out the full importance and the wide applicability of the law. This he has done in two recent publications with an enthusiasm which can hardly fail to prove contagious. There is little danger, I think, of Mendel's discovery being again forgotten.

1. *The law of dominance.* When mating occurs between two animals or plants differing in some character, the offspring frequently all exhibit the character of one parent only, in which case that character is said to be "*dominant*." Thus, when white mice are crossed with gray mice, all the offspring are gray, that color character being dominant. The character which is not seen in the immediate offspring is called "*recessive*," for though unseen it is still present in the young, as we shall see. White, in the instance given, is the recessive character. The principle of heredity just stated may be called *the law of dominance*. The first instance of it discovered by Mendel, related to the cotyledon-color in peas

obtained by crossing different garden varieties. Yellow color of coty-ledons was found to be dominant over green; likewise, round smooth form of seed was found to be dominant over angular wrinkled form; and violet color of blossoms, over white color. Other illustrations might be mentioned both among animals and among plants, but these will suffice.

2. *Peculiar hybrid forms.* The law of dominance is not of universal applicability; Mendel does not so declare, though some of his critics have thus interpreted him. In many cases the cross-bred offspring possess a character intermediate between those of the parents. This Mendel found to be true when varieties of peas differing in height were crossed.

Again, the cross-breds may possess what appears to be *an intensifica-tion of the character of one parent,* as when in crossing dwarf with tall peas the hybrid plant is *taller than either parent,* or as when, in crossing a brown-seeded with a white-seeded variety of bean, the offspring bear beans of a darker brown than that of the brown-seeded parent.

Thirdly, the cross-bred may have a character entirely different from that of either parent. Thus a cross between spotted, black-and-white mice, and albino mice, produces commonly mice entirely gray in color, like the house-mouse. Again, in crossing beans, a variety having yellow-ish-brown seeds crossed with a white-seeded variety yields sometimes black mottled seed, a character possessed by neither parent.

These three conditions may be grouped together by saying — the hybrid often possesses *a character of its own,* instead of the pure character of one parent, as is true in cases of complete dominance. The hybrid character may approximate that of one parent or the other, or it may be different from both. There is no way of predicting what the hybrid character in a given cross will be. It can be determined only by experiment, but it is always the same for the same cross, provided the parents are pure. Often the hybrid form resembles a supposed ancestral condition, in which case it is commonly designated a reversion. Illustrations are the gray hybrid mice, which are indistinguishable in appearance from the house-mouse, and slate-colored pigeons resulting from crossing white with buff pigeons.

3. *Purity of the germ-cells.* The great discovery of Mendel is this: *The hybrid, whatever its own character, produces ripe germ-cells which bear only the pure character of one parent or the other.* Thus, when one parent has the character A, and the other the character B, the hybrid will have the character AB, or in cases of simple dominance, A(B)* or

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* The parenthesis is used to indicate a recessive character not visible in the individual.

B(A). But whatever the character of the hybrid may be, its germ-cells, when mature, will bear *either the character A or the character B, but not both ;* and As and Bs will be produced *in equal numbers.* This perfectly simple principle is known as the law of " *segregation,*" or the law of the " purity of the germ-cells." It bids fair to prove as fundamental to a right understanding of the facts of heredity as is the law of definite proportions in chemistry. From it follow many important consequences.

A first consequence of the law of purity of the germ-cells is polymorphism of the second and later hybrid generations. The individuals of the first hybrid generation are all of one type, provided the parent races are pure. Each has a character resulting from the combination of an A with a B, let us say AB. [In cases of dominance it would more properly be expressed by A (B) or B (A).] But in the next generation three sorts of combination are possible, since each parent will furnish As and Bs in equal numbers. The possible combinations are AA, AB,

TABLE I.

Characters, →	A.	AB.	B.
Plants bearing Flowers in Color,	Magenta Red.	Lavender.	White.
1901, Lot 1	19	27	14
" " 2	9	20	9
1902, " 1	12	23	11
" " 2	14	26	11
Totals	54	96	45
Per cent of whole	29	49+	22

and BB. The first sort will consist of pure As and will breed true to that character ever afterward, unless crossed with individuals having a different character. Similarly the third sort will be pure Bs and will breed true to that character. But the second sort, AB, will consist of hybrid individuals, like those of which the first hybrid generation consisted. If, as supposed, germ-cells, A and B, are produced in equal numbers by hybrids of both sexes, and unite at random, combinations AA, AB, and BB should occur in the frequencies, 1 : 2 : 1. For in unions between two sets of gametes, each A + B, there is one chance each for the combinations AA and BB, but two chances for the combination AB.

If the three forms AA (or simply A), AB, and B are all different in appearance, it will be a very simple matter to count those of each class and determine whether they occur in the theoretical proportions, 1 : 2 : 1. One such case has been observed by Bateson (:02, p. 183) among Chinese primroses (Primula sinensis). An unfixable hybrid variety known as " Giant Lavender," bearing flowers of a lavender color, was produced by crossing a magenta red with a white flowering variety tinged faintly with pink. By seed the hybrid constantly produces plants bearing magenta-red and white flowers respectively, as well as other plants bearing lavender flowers. The numerical proportions observed in two successive seasons are shown in Table I.

The observed numbers, it will be seen, are quite close to the theoretical, 1 : 2 : 1.

In cases wherein the hybrid is indistinguishable from one of the parent forms (i. e. in cases of complete dominance of one parental

TABLE II.

HEREDITY OF COTYLEDON-COLOR AMONG CROSS-BRED PEAS.

Parents crossed.	Offspring.			
	Gen. I.	Gen. II.	Gen. III.	Gen. IV.
G ⎫ ⎪ ⎬ ⎪ Y ⎭	Y(G) ⎰ ⎱	1G . . . . . . ⎧ 2Y(G) ⎰ 3 ⎨ ⎩ 1Y	. G . . . . 1G . . . . . 3 ⎰ 2Y(G) ⎱ 1Y . . . . . . Y . . .	. . G . . G . . Y . . Y

character), only two categories of offspring will be recognizable and these will be numerically as 3 : 1. But further breeding will allow the separation of the larger group into two subordinate classes, — first, individuals bearing only the dominant character; secondly, hybrids; that is, into groups A and A(B), which will be numerically as 1 : 2.

Observed results are in this case very close to theory. Mendel, by crossing yellow with green peas, obtained, as we have seen, only yellow (hybrid) seed. Plants raised from this seed bore in the same pods both yellow seed and green seed in the ratio, 3 : 1. (See Table II.) The green seed produced in later generations green seed

only. It bore only the recessive character. Of the yellow seeds, one in three produced only yellow offspring, i. e. contained only the dominant character; but two out of three proved to be hybrid, producing both green and yellow seed, as did the hybrids of the preceding generation. These are precisely the theoretical proportions, $A + 2 A(B) + B$.

The experiment has been repeated and confirmed by several different observers.

In mice, my friend and pupil, Mr. G. M. Allen, finds the second hybrid generation, obtained by crossing gray with white mice, to consist of gray mice and white mice approximately in the ratio, $3:1$. (See Table III.) The white are pure recessives, producing only white offspring, when bred *inter se*. What portion of the grays are pure dominants has not yet been determined, but we may confidently expect that it will prove to be not far from 1 in 3.

TABLE III.

HEREDITY OF COAT-COLOR AMONG CROSS-BRED MICE OBTAINED BY MATING WHITE MICE (W) WITH GRAY MICE (G).

Parents crossed	Offspring.		
	Gen. I.	Gen. II.	Gen. III.
W ⎱ ⎰ G	G(W)	1W . . . . . . 3 ⎰ 2(?)G(W) ⎱ 1(?)G . . .	. . W . . G

A further test of the correctness of Mendel's hypothesis of the purity of the germ-cells and of their production in equal numbers, is afforded by back-crossing of a hybrid with one of the parental forms. For example, take a case of simple dominance, as of cotyledon-color in peas or coat-color in mice. We have here characters D (dominant) and R (recessive). The first generation hybrids will all be $D(R)$. Any one of them back-crossed with the recessive parent will produce fifty per cent of pure recessive offspring and fifty per cent of hybrids.

For the hybrid produces germ-cells . . . . $D + R$
The recessive parent produces germ-cells . . $R + R$
The possible combinations are . . . . . $\overline{2D(R) + 2R}$

This case has been tested for peas and for mice and found to be substantially as stated.

We have thus far considered only cases of cross-breeding between parents differing in a single character. We have seen that in such cases, no new forms, except the unstable hybrid form, are produced. But when the parent forms crossed differ in two or more characters, there will be produced in the second and later hybrid generations individuals possessing *new combinations* of the characters found in the parents; indeed *all possible combinations* of those characters will be formed, and in the proportions demanded by chance. Thus when parents are crossed which differ in *two* characters, A and B, let us designate the dominant phase of these characters by A, B, the recessive phase by a, b. The immediate offspring resulting from the cross will all be alike, AB(ab),* but the second and later generations of hybrids will contain the stable (i. e. pure) classes, AB, Ab, aB, ab, in addition to other (unstable, or still hybrid) forms, namely AB(ab), A(a)b, and aB(b). In every six-teen second-generation offspring there will be, on the average, one of each of the stable combinations. Two of these combinations will be identical with the parent forms, the other two will be new.

But the difficulty of establishing a stable (i. e. pure) race is greater in this case than in that of one variable character. Only the individual which possesses *both recessive characters* can at once be set aside as pure. For to each of the stable individuals possessing one dominant and one recessive character, there will be *two other individuals, exactly like it in appearance,* but hybrid in one of the two characters. The one pure individual can be distinguished from the two impure individuals only by breeding tests.

Again, nine out of every sixteen of the second-generation hybrids will possess the *two dominant characters,* and so will be in appearance exactly like their parents, the first-generation hybrids. But *only one* of the nine will be *pure* with reference to those characters. Of the remaining eight, four will be hybrid in one character, and four will be hybrid in *both characters* exactly like the entire first generation of offspring.

The greater the number of separately variable characters involved in a cross, the greater will be the number of new combinations obtainable; the greater, too, will be the number of individuals which it will be necessary to raise in order to secure *all* the possible combinations; and the greater, again, will be the difficulty of isolating the pure (i. e.

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* This is Mendel's use of lower-case letters to designate recessive characters, with which I have combined the use of a parenthesis when a character by nature recessive is not visible in the individual.

stable) forms from such as are similar to them in appearance but still hybrid in one or more characters.   Mendel has generalized these statements substantially as follows: In cases of complete dominance, when the number of differences between the parents is n, the number of different classes into which the second generation of offspring fall will be 3^n, of which 2^n will be *pure* (stable); the remainder will be hybrid, though indistinguishable from pure individuals.   The smallest number of individuals which in the second hybrid generation will allow of *one pure individual* to each visibly different class, will be 4^n.   See Table IV.

TABLE IV.

Number of Differences between Parents.	Visibly Different Classes, each containg one Pure Individual.	Total Classes, Pure and Hybrid.	Smallest Number of Offspring allowing one Individual to each Class.	
n	2^n	3^n	4^n	
1	2	3	4	) Tested by Mendel
2	4	9	16	} for peas and found
3	8	27	64	) correct.
4	16	81	256	)
5	32	243	1024	} Calculated.
6	64	729	4096	)

The law of Mendel reduces to an exact science the art of breeding in the case most carefully studied by him, that of entire dominance.   It gives to the breeder a new conception of "purity."   No animal or plant is " pure " simply because it is descended from a long line of ancestors possessing a desired combination of characters ; but *any* animal or plant is pure if it produces gametes of only one sort, even though its grandparents may among themselves have possessed *opposite* characters.   The existence of purity can be established with certainty only by suitable breeding tests (especially by crossing with recessives), but it may be safely assumed for any animal or plant descended from parents which were like each other and had been shown by breeding tests to be pure.

Special cases under the law of Mendel.   It remains to speak of some special cases under the law of Mendel, which apparently are exceptions to one or another of the principles already stated, and which probably result from exceptional conditions known to us only in part.   These special cases have come to light in part through Mendel's own work, in part through that of others.

1. *Mosaic inheritance.* It occasionally happens that in crosses which bring together a pair of characters commonly related as dominant and recessive, the two characters appear in the offspring in patches side by side, as in piebald animals and parti-colored flowers and fruits. The normal dominance apparently gives place in such cases to a balanced relationship between the alternative characters. What conditions give rise to such relationships is unknown, but when they are once secured they often prove to possess great stability, breeding true *inter se*. This, for example, is the case in spotted mice, which usually produce a large majority of spotted offspring. The balanced relationship of characters possessed by the parents is transmitted to the germ-cells, which are, not as in ordinary hybrid individuals D or R, but $\frac{1}{2}$ DR. This has been shown to be the case in spotted mice by G. M. Allen and myself, in a paper published elsewhere. The balanced condition of D and R, which exists in the gamete, is upset when that gamete unites with a pure R (and probably also when it unites with a pure D); for spotted mice bred to white mice regularly gave only uniformly gray or black individuals, after the formula $\frac{1}{2}$ DR $+$ R $=$ D(R).* But an exceptional spotted male, own brother to those which gave the described result, apparently produced gametes D and R as well as others $\frac{1}{2}$ DR, for by white females he had pure white offspring as well as those which were gray or black in color. This result can be expressed by the formulæ : —

$$\begin{array}{lll} \text{Sperm.} & \text{Ovum.} & \text{Offspring.} \end{array}$$

$$\left. \begin{array}{l} \tfrac{1}{2}\,\text{DR} + \text{R} = \text{D(R)}^* \\ \text{D} + \text{R} = \text{D(R)} \end{array} \right\} \begin{array}{l} \text{ordinary gray or} \\ \text{black hybrids.} \end{array}$$

$$\text{R} + \text{R} = \text{R}, \qquad \text{white (pure).}$$

2. *Stable hybrid forms.* This is a case, in some respects similar to the last, which was familiar to Mendel (:70) himself. It sometimes happens, as we have seen, that the hybrid has a form of its own different from that of either parent. To such cases the law of dominance evidently does not apply. In a few cases — Hieracium hybrids (Mendel), Salix hybrids (Wichura) — it has been found that the hybrid form does not break up in the second generation and produce individuals like the grandparents, but breeds true to its own hybrid character. This can be explained only

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* Observations made since the foregoing was written indicate that the offspring in this case are, sometimes at least, $\frac{1}{2}$D(R) · (R). For when an individual of this sort forms gametes, they apparently are, not pure D and R, but $\frac{1}{2}$ DR and R respectively. This hypothesis accounts for the *reappearance* of spotted mice after their disappearance for a generation in consequence of crossing.

on one of two assumptions. Either the germ-cells bear the two charac-
ters in the balanced relationship, $\frac{1}{2}$ AB, as do spotted mice ordinarily, or,
of the two gametes which unite in fertilization, one invariably bears the
character A, the other the character B.

3. *Coupled characters.* This is the phenomenon of correlation of
characters in heredity. It is sometimes found that, in cross-breeding, two
characters cannot be separated. When one is inherited, the other is
inherited also. Thus, in crossing different sorts of Datura (the James-
town weed) it has been found that purple color of stem invariably goes
with blue color of flowers, whereas green stems are constantly associated
with white flowers. Again in mice, rabbits, and most other mammals,
white hair and pink eyes occur together and may not be separated in
heredity. Very rarely, however, as I have observed, an otherwise per-
fectly white guinea-pig has dark eyes; further the ordinary albino guinea-
pig with pink eyes has usually smutty (brown-pigmented) ears, nose, and
feet. These exceptional conditions probably represent stable couplings
of a *part only* of the dominant character (pigmented coat) with the reces-
sive character (white coat), and are similar in kind to the $\frac{1}{2}$ DR character
of the spotted mice. For guinea-pigs do occur entirely devoid of the D
character, i. e. without dark nose, ears, and feet, and with pink eyes.
These doubtless represent the *pure* recessive condition.

Further, coupling may occur between a number of characters greater
than two, so that they form, to all intents and purposes, in heredity, one
indissoluble compound character. Thus, Correns (:00) observed that
in crosses between two species of stocks (Mathiola incana DC. and M.
glabra DC.) the second generation hybrids showed reversion to one or
the other of the parental forms in *all three of the principal differential
characters* studied, viz., hairy or glabrous stems, violet or yellow-white
flowers, and blue or yellow seed. A blue seed always produced a hoary
plant bearing violet flowers; a yellow seed always produced a glabrous
plant bearing yellow or white flowers.

4. *Disintegration of characters.* This is the converse of the foregoing
process. Not only may characters apparently simple be coupled together
in heredity to form composite units of a higher order, but characters
which ordinarily behave as units may as a result of crossing undergo dis-
integration into elements separately transmissible. Thus the gray coat-
color of the house-mouse is always transmitted as a dominant unit in
primary crosses with its white variety; but in the second cross-bred
generation a certain number of *black* mice appear, some or all of which
are probably hybrids. For similar black mice obtained by crossing black-

white with white mice have been shown, by breeding tests, to be hybrids, since on crossing with white mice they produce white mice, black mice, and, in one or two cases, gray mice also. Accordingly black mice clearly belong with grays in the category of dominant individuals [D or D (R)], but they have visibly *only the black constituent* of the gray coat, the remaining constituent, a rufous tint, having been separated from the black in consequence of cross-breeding. There is reason to believe that the rufous constituent may become recessive (i. e. latent) either in the black individuals or in the reverted whites, or in both. It is seen separated from both the black and the white characters, in the chocolate-brown and reddish-yellow individuals obtained in cross-breeding.

A fancier of rabbits tells me that there occurs a similar disintegration of the composite coat-color of the " Belgian hare," when that animal is crossed with ordinary white rabbits, the result being the production of black, yellow, and mottled individuals, in addition to ordinary gray-browns.

The various distinct colors or color patches of the guinea-pig have doubtless originated in a similar way, — by resolution of the composite coat-color of the wild Cavia, upon crossing with an albino sport. This subject is now undergoing investigation.

Correns (:00) mentions a case in plants, which probably belongs in this same category. In crossing the blue-flowered (dominant) Mathiola incana with the yellowish-white flowered (recessive) M. glabra, the second generation recessives produced in some cases pure white flowers, in others yellow flowers. In this case the recessive character, rather than the dominant, underwent disintegration.

5. *Departures from the theoretical ratios of dominants to recessives.* Considerable departures are to be expected when the number of offspring taken into consideration is small, but with increase in the number of offspring examined, the departures should grow less. This is usually found to be true. Mendel's numbers are shown by Weldon (:02) to be well within the limits of probable error. But certain cases have been observed in which departures of a particular sort persist even with considerable numbers of offspring. Thus Allen and I have found the recessive character, white, in mice to be inherited in about three per cent more than the calculated number of cases, while the equally recessive dancing character is inherited in about thirty-three per cent less than the calculated number of cases. These fairly uniform departures indicate, to my mind, a vitality, on the part of the recessive gamete, in one case somewhat superior, in the other much inferior to that of the dominant

gamete. Inferior vitality of gametes of either sort would result in greater mortality and so in a diminished number of individuals derived from such gametes.

Of course other explanations are possible, as, that the two sorts of gametes are *not* produced in equal numbers. More extended investigations of such cases can alone make their meaning clear.

6. *Reversal of Dominance.* Exceptional cases are on record in which crossing of a dominant with a recessive has resulted in the production of *pure* dominants, or recessives, instead of hybrids. Such cases are, I believe, correctly referred by Bateson to the category of "false hybridization" as described by Millardet, a phenomenon akin to parthenogenesis, in which sexual union has served merely to *stimulate one gamete to development* without bringing about its union with the other gamete.

It is possible, however, that there are cases in which one of a pair of characters is sometimes dominant, sometimes recessive. Tschermak (:01) believes that he has found a few such cases among cross-bred beans. Sex and certain other dimorphic conditions found in the higher animals and plants may prove to be cases of this sort.

Acceptance of Mendel's principles of heredity as correct must lead one to regard discontinuous (or sport) variation as of the highest importance in bringing about polymorphism of species and ultimately of the formation of new species.

A sport having once arisen affecting some one character of a species, may by crossing with the parent form be the cause of no end of disintegration on the part of any or all of the characters of the species, and the disintegrated characters may, indeed *must*, form a great variety of new combinations of characters, some of which will prove stable and self-perpetuating. Even if a particular combination of characters is uniformly eliminated by natural selection under one set of conditions, it may reappear again and again, and finally meet with conditions which insure its success.

We now have an explanation of the long-recognized principle that new types of organisms are extremely variable, whereas old types vary little. A new type which has arisen as a sport will cross with the parent form. The offspring will then inherit some characters dominant, others latent, and polymorphism of the race results. Only selection continued through long periods of time will serve to eliminate completely the latent recessives, and so to cause the disappearance of certain aberrant variations.

Bateson makes the pregnant suggestion that even cases of continuous

variation may possibly prove conformable with Mendelian principles. Take, for example, the height of peas. It has been found in certain crosses of a tall with a dwarf variety of pea, that the hybrid has an intermediate height. Now, if the hybrid produces pure germ-cells, dwarf and tall respectively, in equal numbers, the next generation will consist of three classes of individuals, dwarf, intermediate, and tall, in the proportions, 1 : 2 : 1. But if each of the original characters should undergo disintegration, we might get a dozen classes, instead of three, resulting in a practically continuous frequency-of-error curve.

Summary.

1. The basic principle in Mendel's discoveries is that of the purity of the germ-cells ; in accordance with this a cross-bred animal or plant produces germ-cells bearing *only one* of each pair of characters in which its parents differ. From it follow the occurrence in the second and later hybrid generations of a definite number of forms in definite numerical proportions.

2. Mendel's principle of dominance is realized in the heredity of a considerable number of characters among both animals and plants. In accordance with this principle, hybrid offspring have visibly the character of only one parent or the other, though they transmit those of both parents.

3. In other cases the hybrid has a distinctive character of its own. This may approximate more or less closely the character of one parent or the other, or it may be entirely different from both. Frequently the distinctive hybrid character resembles a lost ancestral character. In some cases of this sort, as in coat-color of mammals, the hybrid character probably results from a recombination of the characters seen in one or both parents, with certain other characters latent (that is, recessive) in one parent or the other.

4. There have been observed the following exceptions to the principle of dominance, or to the principle of purity of the germ-cells, or to both : —

(*a*) Mosaic inheritance, in which a pair of characters ordinarily related as dominant and recessive occur in a balanced relationship, side by side in the hybrid individual and, frequently, but not always, in its germ-cells also. This balanced condition, once obtained, is usually stable under close breeding, but is readily disturbed by cross-breeding, giving place then to the normal dominance.

(*b*) Stable (self-perpetuating) hybrid forms result from certain crosses. These constitute an exception to both the law of dominance and to that

of purity of the germ-cells. For the hybrid is like neither parent, but the characters of *both* parents exist in a stable union in the mature germ-cells produced by the hybrid.

(*c*) Coupling (i. e., complete correlation) may exist between two or more characters, so that they form a compound unit not separable in heredity, at least in certain crosses.

(*d*) Disintegration of characters apparently simple may take place in consequence of cross-breeding.

(*e*) Departures from the expected ratios of dominants to recessives may be explained in some cases as due to inferior vigor, and so greater mortality, on the part of dominants or recessives respectively.

(*f*) Cases of apparent reversal of dominance may arise from "false hybridization" (induced parthenogenesis). Possibly in other cases the determination of dominance rests with circumstances as yet unknown.

5. Mendel's principles strengthen the view that species arise by discontinuous variation. They explain why new types are especially variable, how one variation causes others, and why certain variations are so persistent in their occurrence.

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