

the giving up of the idea of relying upon private effort.

That we lose most where the State does least is known to Mr. Chamberlain, for in his speech, to which I have referred, on the University of Birmingham, he said: "As the importance of the aim we are pursuing becomes more and more impressed upon the minds of the people, we may find that we shall be more generously treated by the State."

Later still, on the occasion of a visit to University College School, Mr. Chamberlain spoke as follows:

"When we are spending, as we are, many millions—I think it is 13,000,000*l.*—a year on primary education, it certainly seems as if we might add a little more, even a few tens of thousands, to what we give to University and secondary education" (*Times*, November 6, 1902).

To compete on equal grounds with other nations we must have more universities. But this is not all—we want a far better endowment of all the existing ones, not forgetting better opportunities for research on the part of both professors and students. Another crying need is that of more professors and better pay. Another is the reduction of fees; they should be reduced to the level in those countries which are competing with us, to say, one-fifth of their present rates, so as to enable more students in the secondary and technical schools to complete their education.

In all these ways, facilities would be afforded for providing the highest instruction to a much greater number of students. At present there are almost as many *professors and instructors* in the universities and colleges of the United States as there are *day students* in the universities and colleges of the United Kingdom.

Men of science, our leaders of industry, and the chiefs of our political parties all agree that our present want of higher edu-

cation—in other words, properly equipped universities—is heavily handicapping us in the present race for commercial supremacy, because it provides a relatively inferior brain-power which is leading to a relatively reduced national income.

The facts show that in this country we can not depend upon private effort to put matters right. How about local effort?

Anyone who studies the statistics of modern municipalities will see that it is impossible for them to raise rates for the building and upkeep of universities.

The buildings of the most modern university in Germany have cost a million. For upkeep the yearly sums found, chiefly by the State, for German universities of different grades, taking the incomes of seven out of the twenty-two universities as examples, are:

1st Class.....	Berlin.....	£	130,000
2nd Class.....	{ Bonn.....	}	56,000
	{ Göttingen		
3rd Class.....	{ Königsberg	}	48,000
	{ Strassburg		
4th Class.....	{ Heidelberg	}	37,000
	{ Marburg		

Thus if Leeds, which is to have a university, is contented with the 4th class German standard, a rate must be levied of 7*d.* in the pound for yearly expenses, independent of all buildings. But the facts are that our towns are already at the breaking strain. During the last fifty years, in spite of enormous increases in rateable values, the rates have gone up from about 2*s.* to about 7*s.* in the pound for real *local* purposes. But no university can be a merely local institution. NORMAN LOCKYER.

(To be concluded.)

MENDEL'S LAW OF HEREDITY.*

WHAT will doubtless rank as one of the great discoveries in biology, and in the

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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 center 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 a zoologist, Bateson, two years later, to point out the full importance and the wide applicability of the law. Since then the Mendelian discoveries have attracted the attention of biologists generally. Accordingly a brief statement of their underlying principles may not be without interest to others also.

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 cotyle-

don-color in peas obtained by crossing different garden varieties. Yellow color of cotyledons 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 *intensification 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 those 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 yellowish-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 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 individuals were 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 combinations

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

are possible, since each parent will furnish As and Bs in equal numbers. The possible combinations are AA, AB 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 consist of 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 was exclusively composed. If, as supposed, germ-cells, A and B, are produced in equal numbers by hybrids of both sexes, and unite at random in fertilization, 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 in an experiment 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

TABLE I.

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

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

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.....	G..... 1G.....	...G ...G
		3 { 2Y(G) } 1Y.....	3 { 2Y(G) 1Y.....	...Y ...Y

one parental 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 also 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.) Under self-fertilization, 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, $A + 2 A(B) + B$.

In the case of mice, it has been shown independently by Cuenot (:02) and by the writer's pupil, Mr. G. M. Allen, that the second hybrid generation, obtained by crossing gray with white mice, consists 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 with precision, 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.....	...W 1W
		3 { 2G(W) } 1G.....	3 { 2G(W) 1G

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.... $2D(R) + 2R$

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* respects, 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), AB(b), A(a)B, A(a)b and aB(b). In every sixteen second-generation offspring there will be, on the average, one representing each of the stable combinations. Two of the stable combinations will be identical with the parent forms, the other two will be new. The remaining twelve individuals will be hybrid in one or both characters.

An illustration may help to make this case clear. Among domesticated guinea-pigs, as among mice and rabbits, albinism is recessive with respect to pigmented coat. Further, there occur among guinea-pigs individuals known as 'Abyssinians,' whose

* 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.

coat presents a curious rough appearance, for the reason that the hair stands out stiffly from the body in a number of 'cowlicks' or rosettes. In crosses the Abyssinian or rough coat regularly dominates over the normal or smooth coat. Now let us consider what happens when a cross is made involving both these pairs of Mendelian characters, albinism *vs.* pigmented coat, and smooth *vs.* rough coat. If a white Abyssinian is bred to a pigmented smooth guinea-pig, the young are without exception *pigmented* and *rough*, these being the *dominant* members of the two pairs of characters. But the young of course contain in a latent condition the two recessive characters, white coat and smooth coat, which fact may be indicated by designating them as already suggested, AB(ab) [A, a referring to the rough or smooth character of the coat and B, b to its color].

These primary hybrids, if bred *inter se*, will produce young of four different sorts, viz., rough pigmented, rough white, smooth pigmented and smooth white. A certain number of the animals of each sort will *breed true*, *i. e.*, will produce only their own sort when mated to animals like themselves. Theoretically there should be one *pure* individual of each of the four sorts in a total of sixteen young. The four pure individuals answer to the classes AB, Ab, aB, ab already mentioned.

But, besides these pure individuals, there will occur in three of the four classes *impure* or hybrid individuals, which will transmit to some of their young the dominant character or characters which they themselves possess, but to others of their young the corresponding recessive character or characters. Only the class of smooth white animals (of which there should be one in sixteen young) contains none but pure individuals, for they bear

the two recessive characters (ab), and so conceal no hidden recessives. They may at once be set aside as pure. But in the other three classes nothing but actual breeding tests will serve to show which individuals are pure and which impure or hybrid. To each *pure* individual possessing one dominant and one recessive character there will be two others, *exactly like it in appearance*, but hybrid in one pair of characters. This statement applies to the two classes, rough-white and smooth-pigmented, in which the impure individuals would be designated A(a)b and aB(b) respectively. Such impure animals bred *inter se* would produce, in the case of rough-white parents, both rough-white and smooth-white offspring, and in the case of smooth-pigmented parents, both smooth-pigmented and smooth-white offspring.

In the class of rough-pigmented second-generation offspring, which combines the two dominant characters, there will be to each pure individual (AB) eight which are impure in one or both characters. Two of the eight will be hybrid in one character only, as in the rough *vs.* smooth character they form the class A(a)B; two other individuals will be hybrid in the other character, albino *vs.* pigmented, forming the class AB(b); while the remaining four will be hybrid in *both* characters, exactly like the entire first generation of offspring, AB(ab).

The task of the practical breeder who seeks to 'establish' or 'fix' a new variety, produced by cross-breeding, in a case involving two variable characters, is simply the isolation and propagation of that one in each sixteen of the second-generation offspring which will be *pure* as regards the desired combination of characters. Mendel's discovery by putting the breeder in possession of this information enables him to attack his problem systematically, with

confidence in the outcome, whereas hitherto his work, important and fascinating as it is, has consisted largely of groping for a treasure in the dark.

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.*, 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 Containing One Pure Individual.	Total Classes, Pure and Hybrid.	Smallest Number of Offspring Allowing One Individual to Each Class.	
<i>n</i>	2^n	3^n	4^n	
1	2	3	4	} Tested by Mendel for peas and found correct.
2	4	9	16	
3	8	27	64	
4	16	81	256	} Calculated.
5	32	243	1024	
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 imperfectly. 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 DR. This has been shown to be the case in spotted mice by Mr. Allen and myself, in a paper published elsewhere. (Castle and Allen, :03.)

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 on one of two assumptions. Either the germ-cells bear the two characters in the balanced relationship, AB, as do those of spotted mice, or, of the two gametes which unite in fertilization, one invariably bears the character A, the other the character B. Of the two explanations, the former seems at present much the more probable.

3. *Coupled Characters.*—This is the phenomenon of correlation of characters in heredity. It is sometimes found that, in cross-breeding, two characters can not be separated. When one is inherited, the other is inherited also. Thus, in crossing different sorts of *Datura* (the Jamestown 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 commonly occur together and may not be separated in heredity. Very rarely, however, as I have observed, an otherwise perfectly white guinea-pig has dark eyes; further the ordinary albino guinea-pig

with pink eyes has usually smutty (brown-pigmented) ears, nose and feet; and a race of mice with pink eyes, though partially pigmented coat, has formed the basis of some recent important experiments in heredity conducted by Darbishire (:02, :03) at Oxford, England. These exceptional conditions probably represent stable couplings of a *part only* of the dominant character (pigmented coat) with the recessive character (white coat), and are similar in kind to the DR character of spotted mice.

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 disintegration 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 Men-

delian 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 follows 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 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.

BIBLIOGRAPHY.

BATESON, W.

- :02. 'Mendel's Principles of Heredity, a Defence.' With a Translation of Mendel's Original Papers on Hybridization. 12mo, 212 pp. Cambridge. [England. Contains bibliography and portrait of Mendel.]

BATESON, W., AND SAUNDERS, E. R.

- :02. 'Experimental Studies in the Physiology of Heredity.' Reports to the Evolution Committee of the Royal Society. Report I., 160 pp. London.

CASTLE, W. E., AND ALLEN, GLOVER M.

- :03. 'The Heredity of Albinism.' *Proc. Am. Acad. Arts Sci.*, Vol. 38, pp. 603-622.

CORRENS, C.

- :00. 'G. Mendel's Regeln über das Verhalten der Nachkommenschaft der Rassenbastarde.' *Ber. deutsch. bot. Gesellsch.*, Jahrg. 18, pp. 158-168.

CUÉNOT, L.

- :02. 'La loi de Mendel et l'hérédité, de la pigmentation chez les souris.' *Compt. Rend.*, Paris, Tom. 134, pp. 779-781.

DARBISHIRE, A. D.

- :02. 'Notes on the Results of Crossing Japanese Waltzing Mice with European Albino Races.' *Biometrika*, Vol. 2, Pt. 1, pp. 101-104, 4 figs.

DARBISHIRE, A. D.

- :03. 'Second Report on the Results of Crossing Japanese Waltzing Mice with European Albino Races.' *Biometrika*, Vol. 2, Pt. 2, pp. 165-173, 6 figs.

MENDEL, G.

- :66. 'Versuche über Pflanzenhybriden. *Verh. Naturf.-Vereins in Brünn*, Bd. 4, Abh., pp. 3-47. (Translation in Bateson, :02.)

MENDEL, G.

- :70. 'Ueber einige aus künstlicher Befruchtung entnommenen *Hieracium-Bastarde*.' *Verh. Naturf.-Vereins in Brünn*, Bd. 8, Abh., pp. 26-31. (Translation in Bateson, :02.)

TSCHERMAK, E.

- :00. 'Ueber künstliche Kreuzung bei *Pisum sativum*.' *Zeitsch. f. landwirths. Versuchswesen in Oester.*, Jahrg. 3, pp. 465-555.

TSCHERMAK, E.

- :01. 'Weitere Beiträge über Verschiedenwerthigkeit der Merkmale bei Kreuzung von Erbsen und Bohnen.' (Vorläufige Mittheilung.) *Ber. deutsch. bot. Gesellsch.*, Jahrg. 19; pp. 35-51.

VRIES, H. DE.

- :00. 'Sur la loi de disjonction des hybrides.' *Compt. Rend.*, Paris, Tom. 130, pp. 845-847.

VRIES, H. DE.

- :00. 'Das Spaltungsgesetz der Bastarden.' *Ber. deutsch. bot. Gesellsch.*, Jahrg. 18, pp. 83-90.

WELDON, W. F. R.

- :02. 'Mendel's Laws of Alternative Inheritance in Peas.' *Biometrika*, Vol. 1, pp. 228-254, pl. 1, 2.

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WILBUR CLINTON KNIGHT.

THE subject of this sketch was born on a farm at Rochelle, Illinois, December 13, 1858. Early in his boyhood his parents, Mr. and Mrs. David A. Knight, removed to a farm at no great distance from Lincoln, Nebraska. Here he grew to young manhood, gaining the strength of body and mind which is so often developed in unfettered country life. Self-reliance and strength of character came to him in the struggle that he, in common with the other members of the family, had put forth in what was then the new west, in order to wrest from nature the daily bread. Life in all of its forms, and the hills and rocks appealed strongly to him. By the time that he had secured such education as the country school afforded he had also become more than ordinarily familiar with the fauna, the flora and the geological formations of his neighborhood.

Being unusually fond of athletic sports, of fishing and of hunting, he led many a merry party in these pursuits, frequently to the complete exhaustion of most of his fellows. In more recent years, his many friends who at one time or another shared