Heredity and Sex*

Mendelism and Some of Its Recent Developments

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THE history of science is as full of episodes replete with "human interest" as is the history of nations. Not the least of these is the story of Gregor Mendel, a peasant, later a monk, and finally Abbot at Brunn, but now known not for his theology or his kindly deeds to his fellows, but for his patient and successful work in his avocation—the study of heredity. The principal mate-

the mechanism of the germ cell and to sex—are illustrated.

As an illustration of Mendelism in its simplest form we may take the following: The commoner of the two beetles—both undesirable immigrants from Europe—which feed upon our asparagus is *Crioceris asparagi*. It is a small green creature with cream-colored markings. In some individuals these markings consist of three small spots on each wing cover; in other these spots are larger, and the two front ones on each side are joined. Now, if an asparagus beetle having the spots small and separate mates with one having the spots large and joined, the offspring (the "hybrids" or, as this generation is called, F_1) will have the spots large but not joined. If these hybrids mate, the next generation (F_2) will, in the long run, consist of one individual with spots small and separate to two with spots large and separate (hybrids) to one with spots large and joined. This is shown in the insect hall and in the figure 1. Half of the F_2 generation are hybrids, and if mated with similar hybrids will give offspring in these F_2 proportions, 1:2:1. The rest are pure. If spots-small-and-separate be mated with spots-small-and-separate all the offspring will have the spots small and separate, no matter what the previous ancestors were. Likewise spots-joined mated with spots-joined can give only spots-joined.

Although this case has not been as thoroughly studied as the others to be mentioned here, it is cited first because it shows clearly which are hybrids. In the others the law of dominance is so prominent that the simplicity of Mendelism is obscured. Let us analyze this case by means of symbols. We will let S stand for spots small and separate and J for spots joined. As every individual is made up of two parts, maternal and paternal, we will indicate individuals by two letters. The beetles with which we started are therefore SS and JJ . The former produces germ cells each one of which carries the factor S , and each of the germ cells of the latter carries J . United, these make a hybrid individual, SJ . Now the essential point is that a given germ cell can carry the factor for only one condition of a given character. Therefore hybrid asparagus beetles produce two kinds of germ cells, one bearing S and the other J . There are equal numbers of each kind. An S sperm has equal chances of fertilizing an S and a J egg, giving equal numbers of SS and SJ offspring. There are just as many J sperm, and they have equal chances of fertilizing an S and a J egg and therefore we should get a similar number of SJ and JJ offspring. The total would be one SS to two SJ to one JJ . "Q. E. D."

A further test consists in mating pure individuals with hybrids. SS produces only S germ cells, and SJ equal numbers of S and J germ cells. Therefore, there will be an equal number of the combinations, SS and SJ . See Fig. 1.

The ordinary "sour fly" or pomice fly (*Drosophila ampelophila*) has been used more than any other species

of animal or plant in the experimental study of inheritance. The two examples used in the insect hall and shown in Fig. 3 are illustrations of simple Mendelism plus the law of dominance. This is a very slight complication and consists merely in the fact that when two characters are joined in the hybrid only one (the "dominant" one) is evident. The "recessive" character is there however, and half of the germ cells produced

Fig. 1—Illustration of simple Mendelism

Inheritance of color pattern in the common asparagus beetle (*Crioceris asparagi*). The upper experiment shows the result of mating a beetle having spots small and separate with one having spots large and joined. The offspring are hybrids, unlike either parent, but if mated with one another half their offspring will be hybrids, one-fourth pure-blooded and like the original female ancestor, and one-fourth pure-blooded and like the original male ancestor. If one of these pure-blooded offspring now mates with a hybrid, the resulting offspring will be half hybrid and half pure-blooded, as shown in the lower experiment.

rial which he used in this study was the common pea, and his results were published in an obscure journal in 1865. Darwin knew of his work but failed to appreciate its significance. In fact, it remained unnoticed until eighteen years after Mendel had died when, independently but simultaneously, it was brought to our attention, together with important confirmations, by three noted botanists: De Vries, Correns, and Tschermak. Its rediscovery has not only given us a theory of heredity which has revolutionized the practical breeding of plants and lower animals, but also it has given a new impetus to the experimental study of evolution and, through the "eugenics" movement, bids fair to play an important part in the development of human society. It is fitting, therefore, that the American Museum should arrange exhibits illustrating the principles of Mendelism. In the Darwin hall of the American Museum, features of the Mendelian law of heredity are shown by means of peas and rats, while in the insect hall not only Mendelism, but also the later developments of Mendelism—its relation to

Fig. 2—Inheritance of color in peas

Mendel's classic experiments were made with the common garden pea (*Pisum sativum*). When peas of yellow seed color were crossed with those of green seed color, the peas of the resulting plants were all yellow. When these yellow peas were mated together the peas of the resulting plants were one-fourth pure yellow seed color, two-fourths yellow hybrids, and one-fourth pure green. Of these the pure yellows and greens bred true, the hybrids continuing to give half hybrids and half pure as before.

by such a hybrid bear only the recessive character. If a pomice fly having aborted wings of a certain kind be mated with a pure normal-winged fly, all the offspring (hybrids, or F_1) will have normal wings, for normal wing is dominant and aborted wing is recessive. If these hybrids be mated together we shall get in the F_2 generation, one pure normal-winged to two hybrid (but having normal wings), to one pure aborted-winged. More briefly, the ratio is three normal-winged to one aborted-winged. Although the eye can not distinguish between the two kinds of normal-winged F_2 , breeding shows that they exist in the proportions just mentioned. In the second illustration, normal body color is dominant and black is recessive.

Mendel used peas in his own experiments, and in Fig. 2 is shown part of the exhibit in the Darwin hall illustrating these. The pair of characters concerned is yellow seed color (dominant) and green seed color (recessive). In order that this case may be understood in its relation to the zoölogical illustrations, it should be noted that seeds are really young next-generation plants. In this exhibit the fact is emphasized that the extracted dominants and recessives of F_2 and subsequent generations, i.e., the pure offspring of hybrid parents, are really pure. If mated, each to its kind, they carry on their strain indefinitely.

Fig. 3—The law of dominance

Inheritance of wing length (left) and of color (right) in the pomice fly. When two characters are joined in a hybrid, only one (the dominant one) is evident. Normal wing is dominant to aborted wing and light to dark color, so the offspring from a pure normal and an aborted-winged fly will all have normal wings. The recessive character is present however, in half the germ cells of each hybrid, and their mating will produce one pure dominant and two hybrids to one pure recessive, the pure dominant and both the hybrids having normal wings. Similarly in the color series.

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Fig. 4—Mendelism in rats

If a pure gray rat be mated with a white rat the offspring will all be gray, for gray is dominant and white is recessive. In the next generation there will be three grays to one white; the white and one of the grays are pure and will breed true; the other two grays are hybrids.

As illustrations of Mendelism in vertebrates, experiments with the wild, gray and domesticated "fancy" rats¹ are exhibited in the Darwin hall. If a pure gray rat be mated with a white rat the offspring will all be gray, for gray is dominant while white is recessive, and in the F₂ generation there will be three grays to one white (see Fig. 4). This white, however, will be pure. Suppose a breeder had only one white rat, but wished to establish a strain. He could mate it with a wild gray, and although the hybrids would all be gray, he could get pure white individuals either by mating the original white with one of its hybrid offspring, or by mating hybrids with hybrids. In the former case he would get 50 per cent hybrids to 50 per cent pure white (see the asparagus beetle illustration) and in the latter 75 per cent grays (one-third of them pure gray) to 25 per cent pure white.

Let us go a step further and consider what happens if there are two independent pairs of characters. In this connection compare Fig. 3 with Fig. 7. In Fig. 7 it is seen that one of the parents has aborted wings and dark body color while the other is normal with respect to each of these characters. Since light body color and normal wing are dominant, all of the F₁ generation are light and have normal wings. In the F₂ generation one-fourth of the offspring have aborted wings, one-fourth have dark body color, while three-fourths have long wings and three-fourths have light body color. However, there are four different combinations in the ratio of nine light-normal to three light-aborted to three dark-normal to one dark-aborted. Those acquainted with the laws of chance will see that this is the ratio to be expected if twelve light and four dark (3:1) be independent from, and combined in a random fashion, with twelve long and four aborted. The germinal analysis may be given as follows, *L* standing for light color, *d* for dark color, *N* for normal wing and *a* for aborted wing: The recessive condition of the characters is indicated by the small letters. The one parent, *LLNN*, produces germ cells which are all *LN*. The germ cells of the other parent, *ddaa*, are all *da*. Therefore the offspring will all be *LdNa*. These offspring, male and female, will each produce four kinds, (in equal numbers) of germ cells: *LN*, *La*, *dN* and *da*. Suppose the combinations of letters just given to be eggs, and combine them in a random fashion with the four kinds of sperm: *LN*, *La*, *dN* and *da*. *LN* sperm, fertilizing the various kinds of eggs, would produce equal numbers of *LLNN*, *LLNa*, *LdNN* and *LdNa* individuals. Writing out in like fashion the combinations

Fig. 5—Duplex inheritance in rats

The two pairs of characters here involved are black *versus* yellow, and self-colored *versus* hooded, black and self-colored being dominant, respectively, to yellow and hooded. The first-generation offspring are all gray hybrids, each with four different kinds of germ cells, which produce in the following generation four kinds of individuals, as in the case of the pomice flies. One only of each kind is shown.

for the other kinds of sperm and adding the results together, we find we have

$$\begin{aligned}
 1 \text{ } LLNN + 2 \text{ } LLNa + 2 \text{ } LdNN + 4 \text{ } LdNa &= 9 \text{ light-normal,} \\
 1 \text{ } LLaa + 2 \text{ } Ldaa &= \\
 3 \text{ light-aborted,} \\
 1 \text{ } ddNN + 2 \text{ } ddNa &= \\
 3 \text{ dark-normal,} \\
 1 \text{ } dd aa &= \\
 1 \text{ dark-aborted.}
 \end{aligned}$$

In the case of the rats (Fig. 5) only a sample of each class of F₂ individuals is shown. The ratio is nine black-self-colored to three black-hooded to three yellow-self-colored to one yellow-hooded, for black is dominant over yellow and self-colored over hooded.

There is, theoretically, no end to the number of pairs of characters which may be concerned in any one cross, but the principles are the same: a given germ cell carries but one of each pair, and where both

Fig. 6—Inheritance of three pairs of characters

Where three pairs of characters are concerned in a cross there will be eight classes of individuals in the second generation of offspring. The pairs of characters concerned above are black and cream-colored, yellow and cream-colored, and self-colored and hooded (the condition in which all pigmentation is concentrated near the head). Black, yellow and self-colored are the dominants. The eight classes of offspring (of which only samples are shown) are: black-yellow-self (gray), black-yellow-hooded (white with gray hood), black-cream-self (black), black-cream-hooded (black hood), cream-yellow-self (yellow), cream-yellow-hooded (yellow hood), cream-cream-self (cream) and cream-cream-hooded (cream hood).

color in sweet peas, is complicated by the fact that not only are there three pairs of characters, but also that color of any kind, that is any kind but white, can occur only when certain members of two of these pairs come together. One of the white parents had one of these characters and the other had the second; union by crossing gave colored offspring.

Before passing on to the explanation of what may be called the mechanism of Mendelism, a word should be said for the benefit of those who may have read or heard the Mendelian principles given in terms of presence or absence of characters. We may say that a fly's eye is red in the presence of the factor for red, and white in its absence, or we may speak of the pair of characters as red and white. It has seemed better to use the latter alternative here, but the presence-and-absence way of putting it works out well in certain cases and has given rise to some interesting speculations. Thus, Professor Bateson has suggested that all organic evolution has been brought about by the successive dropping out of characters. This seems hard to believe, but certainly the origin of many varieties, whose origin we think we have seen, can be neatly explained in that way.

In order to understand the mechanism of Mendelian inheritance it will be necessary to explain some of the details of cell structure. The bodies of all the higher animals and plants are made up of cells, which are frequently looked upon as units of body structure. The lowest animals and plants consist of but one of these cells. The germ cells, egg or sperm, are merely some of these cells split off from the main mass of body cells, and differentiated so that they may unite and form a new mass of body cells, the new individual. In some cases the egg cell can carry on this process without uniting with the sperm, but in the vast majority of cases among higher animals and plants such union is normally necessary. Within these cells are bodies called chromosomes, the name being given because they stain deeply when treated with certain reagents. The chromosomes have for some time been supposed to be the bearers of heritable characters, and this supposition has now become almost a certainty by reason of Mendelian studies, especially those with the pomice fly, *Drosophila ampelophila*. We are, as yet, in the dark concerning the exact method by which these characters are transmitted, so that "bearers of heritable characters" is in great part a figure of speech, but, at any rate, these characters are somehow bound up with special chromosomes.

Most, and probably all, organisms have a definite number of these chromosomes, although the number is

Fig. 7—Inheritance of two pairs of characters

Since light body color and normal wing are dominant characters, all of the first-generation offspring, from mating a light normal-winged with a dark aborted-winged individual, will be light with normal wings. These hybrids, however, will each produce in equal numbers, four different kinds of germ cells. In the third generation there will therefore be four different kinds of individuals, in the ratio of nine light-normal to three light-aborted to three dark-normal to one dark aborted.

members of a pair come together in the union of two germ cells to form an individual, one of the characters usually dominates over the other. If three pairs of characters are concerned there will be, typically, eight classes of offspring, in the F₂ generation. This is seen in the third exhibit (Fig. 6) illustrating inheritance of color and pattern in rats where, again, only samples of the various classes are shown. Frequently, as in the case of the rats, the breeder is able, by crossing known varieties, to get new or hitherto unknown varieties in F₂; that is, new combinations are made. The exhibit in the American Museum showing inheritance of flower

¹The rats shown are largely from the important experiments of Professor W. E. Castle, of Harvard, who kindly outlined this portion of the exhibit. The rest of the rats were obtained from the New York Zoological Park through the courtesy of Mr. Dittmars.

not always the same in both sexes. In the pomice fly the number is the same (eight) in each sex, but one of the chromosomes (the "Y") of the male seems to carry maleness and not, as far as is known, any other character. When it is present the individual is a male. It is, however, paired in the body cells of the males with a chromosome which does carry factors for certain body characters, and this other chromosome may be called X. In each of the female body cells there is a pair of these X chromosomes but no Y. When a body cell destined to become a germ cell differentiates, the result of the rather complicated process may be stated simply by saying that it breaks in two, making two nearly similar cells. In the case of the male, the Y chromosome goes to one half, i. e., to one sperm, and the X chromosome to the other. Each egg has an X chromosome. If a sperm having a Y chromosome enters an egg, the union will have one X and one Y and the resulting individual will be a male. However, if a sperm having an X chromosome enters an egg, the union will have X paired with X; there will be no Y and the resulting individual will be a female. Since the chances are equal that an egg will be fertilized by a Y-bearing sperm or by an X-bearing sperm the determination of sex is a random matter; it depends upon which sperm enters and not at all upon the mother; and the number of each sex will, in the long run, be equal. All this is, of course, subject to amendment by further investigation, and too sweeping generalizations should not be made, but it, or a similar relation, seems to hold for other strictly bisexual animals and it is the only explanation for the following, among other, facts:

A few pomice flies were found having white eyes instead of red. This white condition is recessive to red but in inheritance the proportions are not those of simple Mendelism. In what has gone before nothing was said about sex, because characters which have been previously mentioned occur without regard to it. This particular eye color however, is one of a number of characters which are "sex linked." If a white-eyed male be mated with a pure red-eyed female (see Fig. 8), all the offspring, both male and female, will have red eyes. If these offspring be mated with one another, all the females of the next generation will have red eyes, but half of the males will have white eyes and only half will have red eyes. On the other hand, if a red-eyed male be mated with a white-eyed female (see Fig. 9), all the male offspring will have white eyes and all the female offspring will have red eyes. This is what has been called "criss-cross" inheritance—the sons being like their mother and the daughters like their father. If these offspring be mated with one another, half of the male and half of the female offspring will have white eyes, the remainder having red eyes.

The explanation is as follows: This pair of characters, red eye *versus* white eye, is associated with the X, or sex, chromosome. In the first case mentioned the female was pure with respect to this eye-color character; that is, both of the X chromosomes carried the factor for red eye color (see Fig. 8). The male, since it showed the recessive character, must have been pure with respect to white eye color and, furthermore, all males are necessarily pure with respect to this particular pair of eye colors, and also with respect to all other sex-linked characters, since they have but one X chromosome, and since that chromosome, like any other, can bear the factor for only one of a pair of characters. All of the eggs, in this mating, carried the factor for red eye color. Half of the sperm carried the factor for white eye color and the other half had no factor concerned with this pair of characters. If a sperm bearing the factor for white eye color united with an egg, the offspring would be a hybrid since it contained factors for both eye colors, but, since red is dominant over white in this case, this individual would show the red color. It would also be a female, since the union which produced it was with a sperm having an X chromosome. If a sperm not bearing the X chromosome (that is, one with the Y) united with one of the eggs, all of which bore the factor for red eye color, the result would be a male pure with respect to red eye color, since the only factor concerned with this pair of characters came with the egg and was red. In other words, all the females of this generation had red eyes and were hybrids with respect to eye color, while all the males had red eyes and were pure with respect to eye color. Half of the eggs which go to produce the next generation bear the factor for red eye color, and the other half bear the factor for white eye color. Half of the sperm have X chromosomes bearing the factor for red eye color, and the other half have no X chromosomes, and thus have no influence upon eye color. Taking up the first class of sperm, namely, those bearing the X chromosomes: they will, when uniting with an egg, produce female individuals and, since half of the eyes have the factor for red while the other half have the factor for white, half of the resulting females will be pure red, while the other half will be hybrid, but will have red eyes because red is

Fig. 8—Sex-Linked Inheritance

White eye color in the pomice fly is one of a number of characters which are sex-linked. The diagram represents the chromosomes of the pomice fly, circles referring to body cells and ovals to germ cells. The sex chromosomes are shown above and below the ordinary chromosomes (see text), the factor for eye color which each one carries being indicated by an initial. The odd-shaped figure is the "Y" chromosome. When this is present the individual is a male.

dominant over white. In other words, all of the females of this generation show red eyes. When the sperm lacking X chromosomes unites with the eggs, half of which have the factor for red in their X chromosomes and the other half white, the result will be males, half of which will be pure red and the other half of which will be pure white. This gives us the result stated above; namely, all the females and half of the males red-eyed while the other half of the males are white-eyed. This case may perhaps be more readily understood by reference to Fig. 8, and Fig. 9 shows the details of the second case mentioned above, which involves what is known as "criss-cross" inheritance.

The relatively complicated "sex-linked" inheritance just explained became simple when the explanation was

Fig. 9—Criss-cross sex-linked inheritance

If a red-eyed male be mated with a white-eyed female, all the male offspring will have white eyes and all the female offspring red eyes; if these be mated with one another, half of the male and half of the female offspring will have white eyes, the remainder having red eyes.

found, and comes near to demonstrating that there is a relation between heritable characters and chromosomes. It would probably be carrying scientific scepticism too far to continue doubting that it is a causal relation. Ordinary Mendelian characters, that is, those which come out in F_2 in the 3:1 ratio, are related to or borne by the ordinary chromosomes, that is, those chromosomes which are alike and paired in each sex. The interested reader may make diagrams, similar to the ones given here, which will show the mechanism graphically. Now that we think we know where the something which transmits a given character lies in the germ cell, we begin to wonder harder than ever what that something is and how it does it. A number of big steps have been taken in the explanation of heredity and, although the goal is still far ahead, by looking back over the ground already covered we are encouraged to believe that it will finally be reached.

Electric and Hydraulic Transmission

DEALING with the subject of Hydraulic Transmission before the Institution of Automobile Engineers, London, Mr. F. Leigh Martineau said that "an apt comparison could be drawn between a hydraulic transmission and an electric transmission, as the two are similar in many respects. In an electric transmission the essential elements are: (1) The prime mover driving—(2) a generator; (3) a conductor system; (4) an electric motor operating—(5) the driving wheels. So in a hydraulic transmission these elements become:—(1) The prime mover driving—(2) a pump; (3) a pipe system; (4) a hydraulic motor operating—(5) the driving wheels. Their operations may be compared as follows: In the former, the prime mover drives the generator and converts its energy into "electric energy," which is conveyed by the conductor system to the electric motor, where it is reconverted for use at the driving wheels. In the latter case, the prime mover drives the pump and converts its energy into "pressure energy," which is conveyed by the pipe system to the motor, where it is reconverted for use at the road wheels. The claims in favor of electric transmission, however, are, that it is usually more economical, is easily applied at considerable distances from the source of energy supply, and requires considerably less attention than the hydraulic system in regard to upkeep.

However, Mr. Martineau's main interest was with the different types of hydraulic transmission in manufacturing processes of one kind or another. For this purpose the author held that the radial rotating plunger and the axial rotating plunger types of pumps were best suited, because, he declared, experience seemed to show "that for hydraulic transmission to be effective in practice it is necessary to run at high pressure and with small volume, so that the hydraulic losses may be as low as possible, and the oil by this means kept cool; this will increase the mechanical and slip losses, but the net result will be better, and such heating as occurs will be as much in metal of high conductivity as in oil of low conductivity." While with the radial rotary pumps good material and workmanship are essential, they present the advantage of being easily and cheaply produced in quantities, having very few parts, and most of the work on them being cylindrical, can be carried out by grinding.

As regards hydraulic transmission for automobiles, especially of the heavy tractor and other heavy vehicle types, Mr. Martineau has great hopes for the future. He does not consider that it need be heavier than gear transmission, for "it must be remembered that as a rule the fly-wheel clutch, gear box, and countershaft brake can be totally eliminated from the chassis and replaced by two units in one case, which is mostly revolving weight, and will perform all the functions of the parts mentioned, with the added advantages of being able to make use of the whole of the engine power all the time during acceleration, using all the engine power at its most efficient speed on inclines, and having at command an absolutely steady retarding effect which converts surplus energy into heat without causing wear. By using high quality materials and good design the weight of such a transmission can be the same as its equivalent gear box, etc." He thought that there should not be any increase of cost. The question of complication had to be considered from the point of view of the manufacturer and the user. "The manufacturer," he argued, "will have fewer unlike parts to produce, but will have to make more like parts per car; this would seem to indicate simplicity and not complication from his point of view. The user has less to look after and no adjustments or adjustable parts to look after, but he has to keep the case full of oil to a certain mark, and that is all; this does not appear to show complication from his point of view."—*The Practical Engineer*.