A LECTURE ON MENDELISM

Gregor Mendel

[Frontispiece.

A LECTURE ON MENDELISM

BY

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WITH NUMEROUS ILLUSTRATIONS

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INTRODUCTION

The following Lecture is published at the earnest request of several friends who are interested in the subject and who heard it delivered as one of a series of "Science Lectures for the People" early in the present year.

I have to thank Mr. Bateson and Mr. Punnett for kindly allowing me to include their portraits and also must acknowledge my indebtedness to their works on Mendelism for many of the statements contained in this lecture.

H. Drinkwater

Wrexham,
Sept. 1910.

A LECTURE ON MENDELISM

It is never easy, and sometimes impossible, to explain the facts of any science without using its technical language. For technical terms used by scientists are not, as is commonly supposed, arbitrary conventions designed for the exclusion of the layman, but are really abbreviations and simplifications which enable the student to handle in single terms complicated sets of ideas and associations. I will, however, do my best to avoid these technicalities and will only use them when their content has been made clear by the course of the narrative.

As Darwinism is the theory of the origin of species which takes its name from Charles Darwin, so by Mendelism we mean the biological theory of heredity first propounded by Mendel.

Gregor Mendel was born on the 27th July, 1822, at Heinzendorf in Austria. His parents were peasant farmers. They were enabled to send him to Vienna to pursue his studies, and there he took a University degree. When twenty-one years old he joined the Augustinian Order, and three years later was ordained priest. Soon afterwards he removed to Brünn, a few miles north of Vienna, and here he taught natural science in the Realschule from 1853 to 1868, when he was appointed abbot of the Monastery.

During the years he was teaching science in the Monastery School at Brünn, he spent a great deal of time in his little garden, working quietly, patiently, and alone, engaged in his favourite hobby, the cultivation of the edible and the sweet pea. He made careful observations, and kept exact records of about 10,000 plants which he had cultivated. He was well versed in other branches of science, especially meteorology.

Eventually he became president of the Brünn Society of Naturalists.

In 1866 he published an account of his observations on Peas, but the scientific world of Germany did not appreciate their importance, and no one in England seems to have heard anything about them. His work was indeed lost sight of, until it was re-discovered by Prof. **De Vries** of Amsterdam about the beginning of the present century.

In 1902 Prof. Wm. **Bateson** of Cambridge translated Mendel's monograph into English, and published it under the title *Mendel's Principles of Heredity.*

Mendel died in 1884, at the age of sixty-two years.

That branch of science which Mendel founded is concerned with living things—both animals and plants—that is, with Biology. Mendel's work has supplied to Biology a key or guide which may be compared to the mariner's compass; for, just as by the aid of the compass the mariner is able to take the most direct course from one place to another, so, by following Mendel's method, the biologist is now able to achieve results much more quickly, and with greater certainty than hitherto.

Mendel's work constitutes "one of the most fascinating chapters in the history of science." It is interesting not only to the theoretical biologist, but will, I believe, before long be recognized as of great economic, commercial and social importance.

I hope to be able to show that each one of you can, if you like, make observations without cost, and with comparatively little trouble, by which you may not only test the truth of the laws which I shall explain to you, but you may be able to contribute some useful facts. "Mendel's

Professor Bateson

[To face p. 2.

clue has shown the way into a realm of nature which, for surprising novelty and adventure, is hardly to be excelled. It has led us into a new world the very existence of which was unsuspected before." I shall first show you how Mendel gradually developed his theories, and then proceed to describe some of the later results achieved by his followers.

Let us first consider **Mendel's Method.**

His practice was to select two plants, such as two peas, which *differ in some well-marked character*—such as height of stem, colour of flowers, or shape and colour of the seeds, and he produced offspring from these contrasted plants, using one as the male and the other as the female parent.

In order that this may be clearly understood it is necessary to know how plants are normally reproduced; and in case there may be some one present who does not understand this, it will be well briefly to describe the process. Almost any plant will answer the purpose, but we will take a primrose shown in section in Fig. 1. Within the tube of the flower (the corolla), and attached to it, are some small bodies called *anthers*, which contain a fine powder called *pollen*. When the anther is ripe it bursts, and the pollen becomes dispersed. In the very centre of the flower is the *pistil*, surmounted at the top by a little knob called the *stigma*, which is generally covered with a sticky juice.

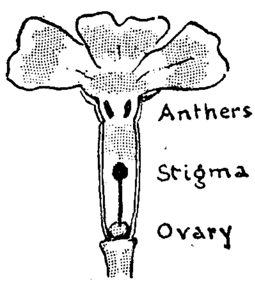


Fig. 1.

The lowest part of the pistil is called the *ovary*—a hollow chamber containing small bodies called *ovules*. These ovules eventually develop into ripe seeds, as a result of uniting with the pollen contained in the anthers.

How does the pollen from the anthers reach the ovules in the closed ovary? When the anther bursts, and the liberated pollen is scattered about, some of it alights on the stigma, and is retained there by the sticky juice (Fig. 2). Very soon the pollen grain begins to shoot out little finger-like processes called "pollen-tubes," which grow down the

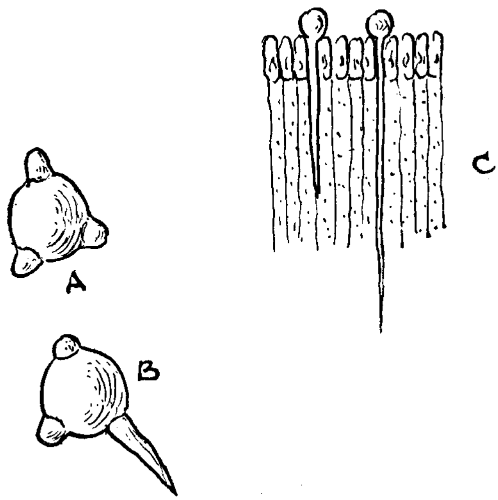


FIG. 2.

A and B are pollen grains with commencing "pollen tubes."
C—Section (vertical) of stigma; showing two pollen grains resting on the upper surface, with their downward growing tubes.

whole length of the pistil, until they eventually reach the ovules. The pollen-tube then enters an ovule, and the two bodies (pollen grain and ovule) become blended into one body, and a ripe seed is the result of the union.

The union of pollen grain with ovule constitutes what is termed "fertilization": the pollen is said to fertilize the ovule; and without the addition of the pollen the ovules will not ripen into "seeds." The pollen is the male element, the ovule is the female element. We may have "self-fertilization," and "cross-fertilization." When pollen fertilizes the ovules of its own flowers, we get "self-fertilization," but the pollen of one flower may be carried by such insects as bees, butterflies and moths to another flower, and effect "cross-fertilization." If the pollen from A (Fig. 3) fertilizes the ovules of B, or if the pollen from B fertilizes the ovules of A we get cross-fertilization.

Gardeners sometimes effect cross-fertilization, or "crosses," by placing the pollen from one flower on to the stigma of another flower.

The flower from which the pollen is derived is the male parent; that which contains the ovules (and seeds) is the female parent.

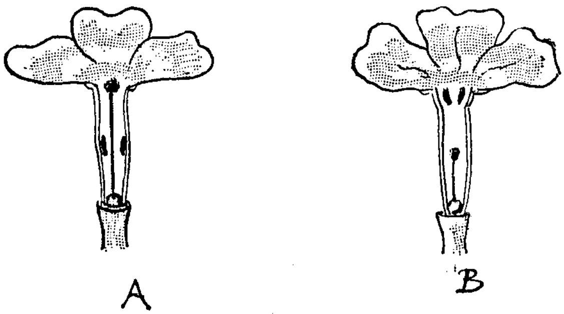


FIG. 3.
THE TWO TYPES OF PRIMROSE.

Male and female may be represented by the letters M (male) and F (female), but they are best represented by certain astronomical signs employed by scientists of all countries—

♂ stands for male;
♀ stands for female.

The male and female *elements*, the pollen grains and ovules, are now called "gametes," which means marrying-cells, but it will be easier to follow me if I use the better-known term "germ-cells." The germ-cells of plants, then, are the pollen grains and ovules. The same term (germ-cells) is also applied to animals; the process of reproduction is essentially the same in them as it is in plants.

Reproduction or fertilization may be represented in diagrammatic form thus—

♀ × ♂

The cross (×) is to be read as "fertilized by." This therefore shows that a female germ-cell is fertilized by a male germ-cell. A vertical line placed under the cross points to the offspring which results from the fertilization, a simple circle indicating the offspring without showing the sex. Thus—

$$\begin{array}{c} ♀ \times ♂ \\ | \\ \circ \end{array}$$

When the two germ-cells which unite in fertilization are derived from two plants which are essentially *similar*, the resulting offspring is said to be "pure-bred." When the two parents show some well-marked *difference*, as in stature or colour of flowers, the offspring is said to be "cross-bred," so far as this particular character is concerned, and such a cross-bred individual is called a "hybrid."

The similarity or difference of the parents may be represented by the sign, thus—

♂ and ♀ represent two similar parents;
♂ and ♀, or ♂ and ♀ represent two parents which differ in some important feature.

$$\begin{array}{c} ♀ \times ♂ \\ | \\ \circ \end{array}$$ represents the production of pure-bred offspring;

$$\begin{array}{c} ♀ \times ♂ \\ | \\ \circ \end{array} \quad \text{or} \quad \begin{array}{c} ♀ \times \\ | \\ \circ \end{array}$$ represents the production of cross-bred or hybrid offspring.

Now, when the parents show a marked difference, what will the hybrid offspring be like? Will it be like one of the parents, and if so, which one? Or will it be intermediate between the two? Clearly it cannot be like both.

This is what Mendel studied experimentally. He sought to discover the Law of Inheritance in these hybrid offspring; in other words, the law or laws governing the resemblance between parent and offspring.

Mendel's method of experimentation was as follows:—

First of all he removed the anthers from a flower just before they were ripe, in order to prevent self-fertilization: this would be the female parent. Then he placed upon its stigma the ripe pollen from another flower, the male parent.

Fig. 4 shows the pollen from a *round*-seeded plant being placed upon the stigma of a plant which produces *angular* seeds. The round seeds and the angular seeds constitute *a pair of contrasted characters.* These angular seeds when ripe were sown, and produced plants which

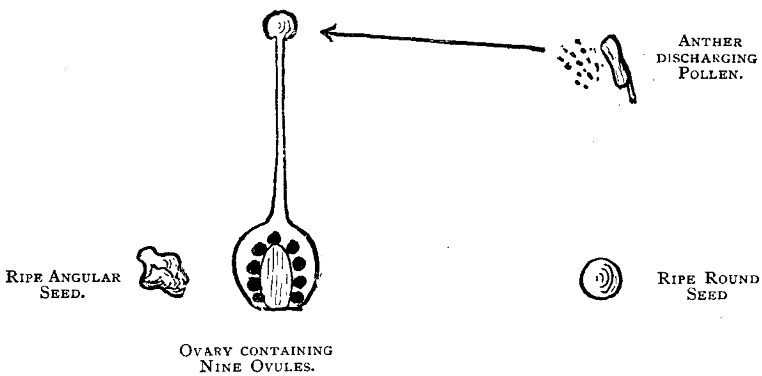


Fig. 4.

Cross fertilization.

were, of course, hybrids, so far as the shape of the seeds was concerned, for the shape differed in the two parent plants.

What Mendel wished to observe in this experiment was the shape of the seeds in this hybrid offspring. Other characters were crossed in a similar manner, such as—

> A tall with a dwarf plant;
> Yellow-seeded with green-seeded plants;
> Coloured flowers with white flowers, and so on.

In each case the male plant showed one character, it mattered not which, and the female showed the contrasted character.

You would probably expect the offspring to be *intermediate* in character between the two parents, but such was never the case. In each instance the offspring exactly resembled *one* parent, *i. e.* it showed only one of any pair of contrasted characters possessed by the parents, to the entire exclusion of the other character.

Thus (Fig. 5) a tall plant crossed with a dwarf produced only tall offspring : *e.g.* the ordinary tall pea was crossed with the cupid variety, which is only 3 or 4 inches high; the ripe seeds were sown, and produced only tall plants—

Coloured flowers crossed with white produced coloured flowers only;

A yellow-seeded plant crossed with a green-seeded one produced only yellow seeds;

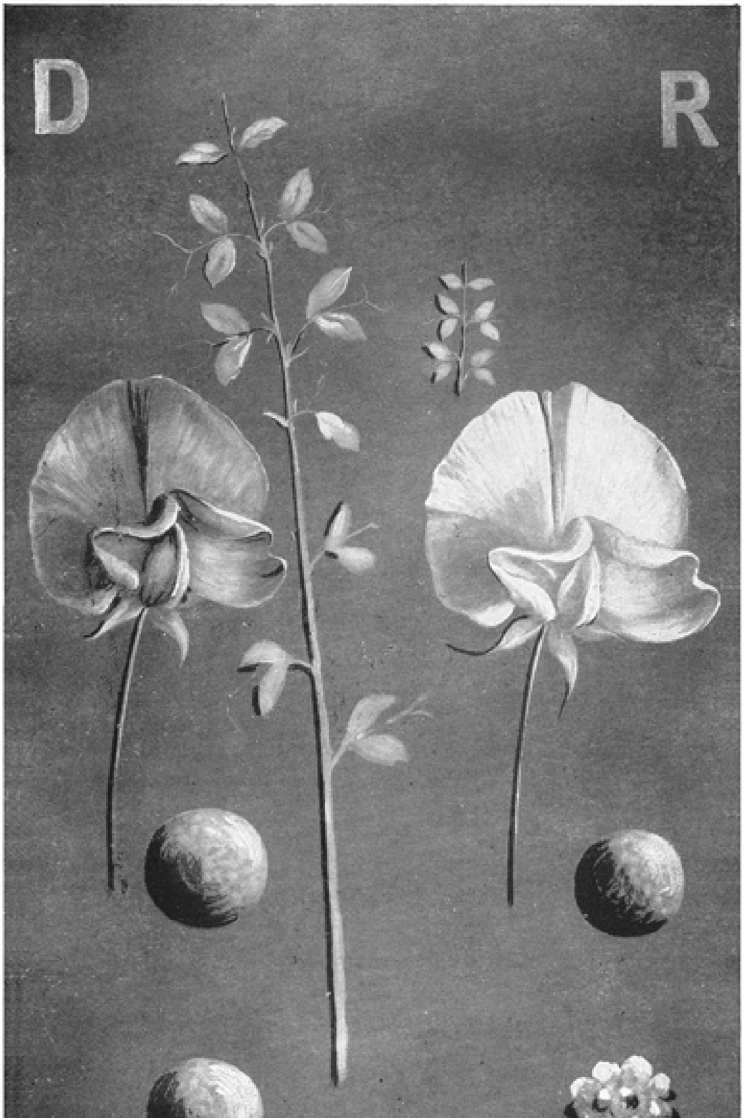
Smooth-seeded crossed with wrinkled-seeded plants gave smooth seeds only.

Thus there was always one of the two contrasted characters in each cross that appeared exclusively in the hybrid offspring, and to this character Mendel applied the term **Dominant**, while that character which did not appear in the offspring he termed **Recessive**.

These two terms ("dominant" and "recessive") you should particularly remember. They are terms for which I am not able to give you any simpler equivalents. You will meet with them repeatedly in the literature of Mendelism.

As a cross between a tall and a dwarf plant produces only tall offspring, tallness is said to be dominant to dwarfness—

Coloured flowers are dominant to white flowers;
Yellow seeds are dominant to green seeds;
Smooth seeds are dominant to wrinkled.



TALL PLANT

DWARF PLANT

COLOURED FLOWERS

WHITE FLOWERS

YELLOW SEEDS

GREEN SEEDS

SMOOTH SEEDS

WRINKLED SEEDS

DOMINANT CHARACTERS | RECESSIVE CHARACTERS

FIG. 5.

[*To face p.* 8.

This is the first of Mendel's results, and I hope it has been made clear to you. It forms the foundation of what follows.

We require some short formula which will express the fact of dominance. If we are considering *stature*, we can employ the following formula—

$$\begin{array}{cl} \text{Tall} \times \text{Dwarf} & \text{(parents)} \\ | & \\ \text{Tall} & \text{(offspring)} \end{array}$$

which means that when a tall plant is crossed with a dwarf all the offspring are tall.

But it is desirable to use some formula which will express the fact of dominance of *any* character, and this can be done by using D to represent a dominant and R to represent a recessive; thus—

$$\begin{array}{c} D \times R \\ | \\ D \end{array}$$

You see this applies not only to stature, but to any of the characters above mentioned.

Another formula very commonly employed is the following—

$$\begin{array}{c} \bullet \times \circ \\ | \\ \bullet \end{array}$$

where the black circle stands for the dominant, and the white circle represents the recessive.

Both the diagrams show that the offspring of certain crosses resemble *one* of the parents, and not the other. The parent which is like the offspring is the dominant parent.

The next step was to breed from these hybrid plants by allowing them to become self-fertilized (the usual method of reproduction in peas). Mendel found that the *two* contrasted characters of the parents reappeared in one or other of the offspring of the hybrids.

Pure-bred tall peas bred amongst themselves breed true, *i.e.* they produce only tall plants; similarly, the dwarfs breed true amongst themselves; but these hybrids, though apparently like the tall parent, do not breed true, but produce both talls and dwarfs. Now this is a most remarkable fact. In the first generation of hybrids the dwarf character has disappeared; apparently it has been destroyed, and yet it reappears in the offspring of these hybrids. The two kinds, the dwarfs and talls produced by the hybrids, appeared, however, in unexpected proportions, for there were always three talls to one dwarf, *i.e.* three dominants to one recessive; and this proportion of three dominants to one recessive holds good, not only for stature, but for whatever pair of contrasted characters be experimented with. This is represented by the following diagram—

```
      D × R
        |
        D
        |
 ---------------
 |   |   |     |
 D   D   D     R
```

It is useful to employ some concise terms to indicate each of these three generations respectively. The first is called the "parental generation," and is indicated shortly by the letter P. The second is the "first filial generation," and indicated by Fj (the word "filial" being derived from the Latin word for son or daughter). The third generation is called the "second filial generation," and is indicated by Fij. If D represents a coloured flower, and R a white one, then in the Fj generation we get only coloured flowers, and in the Fij generation we get three plants bearing coloured flowers to one bearing white flowers, and so on with the other characters named.

Observe! the recessive character (in F_1) has been inherited from a hybrid parent which *looked* exactly like the original dominant parent; it follows, therefore, that this recessive character *must* have been present, though hidden, in the hybrid, and that the hybrid is really different from the original parent, though like it in appearance. This difference may be expressed in the diagram by letting D[R] represent the hybrid, putting the R in brackets, to show that the recessive character is present, though latent, and by mere inspection quite unrecognizable. In other words, the hybrid has a double nature: the dominant and the recessive factors are *both* present in the hybrid, though only the dominant shows. The hybrid is an "impure dominant," and does not breed true to the dominant character. The fact that pure dominants and pure recessives breed true to their respective characters is indicated thus—

$$\begin{array}{c} D \times D \\ | \\ D \end{array} \qquad \text{and} \qquad \begin{array}{c} R \times R \\ | \\ R \end{array}$$

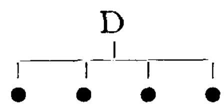
You will see that it is necessary to amend the diagram on page 10 in order to indicate that the F_1 generation consists of impure dominants, thus—

$$\begin{array}{cccc} & & D \times R & \\ & & | & \\ & & D[R] & \\ | & | & | & | \\ D & D & D & R \end{array}$$

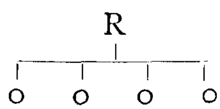
Thus we cannot always tell what the offspring will be like from simple inspection of the parents, for tall plants may produce dwarfs. The results are *not* what would be looked for in accordance with the ordinary view of heredity that "like produces like."

How did Mendel explain these results? Here he showed his genius. He assumed that these hybrids—D[R]—produce two kinds of germ-cells in each sex, two kinds of pollen grain, and two kinds of ovules. One kind possesses the dominant character derived from the dominant parent, the other kind possesses the recessive character of the recessive parent. In other words, the dominant and the recessive properties of the parents are conveyed to separate germ-cells of the hybrid. No single germ-cell can carry both dominant and recessive properties. The germ-cells are not hybrids, though the individuals that produced them may be. This is what Mendel called **Segregation** and it is the most characteristic of his theories.

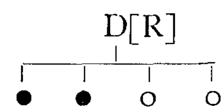
The **Germ-cells** produced by a dominant parent are all purely dominant; those of the recessive parent are all purely recessive; and of those produced by the hybrid, some are dominant and some are recessive. If the dominant is represented by a black circle and the recessive by a white one, then the dominant parent and its germ-cells can be diagrammatically illustrated thus—



The recessive thus—

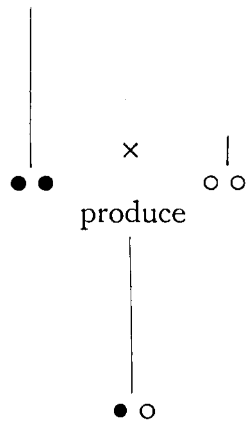


The hybrid thus—



There is only one kind of germ-cells in the dominant, one kind in the recessive, but there are two kinds in the hybrid.

The tall and dwarf pea crossed could be illustrated thus, together with the germ-cells—



According to Mendel, a germ-cell is either purely dominant, or purely recessive, and never partly the one and partly the other—always ● or ○, and never ◐.

I must apologize for repeating myself, but this is the essence of Mendel's theory, and no progress can be made in Mendelism without a clear appreciation of the constitution of the germ-cells.

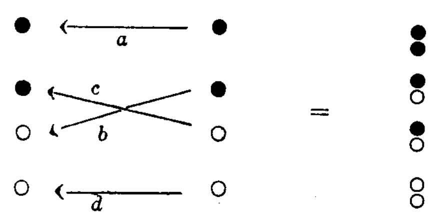
As the character of a plant depends upon the nature of the germ-cells from which it has sprung, it follows that the Fj generation must resemble the dominant parent, and that a tall pea crossed with a dwarf must produce tall offspring; but as the hybrids possess two kinds of germ-cells, their offspring are not of one kind only: some are tall, and others are short (in the Fij generation).

So far, we have seen that Mendel established the fact of dominance; and, secondly, he assumed that hybrids contain germ-cells similar in character to those of both parents.

How did he explain the 3 to 1 ratio in the Fij generation? Now we come to another important doctrine of Mendel—another stroke of genius. Mendel concluded that not only are both dominant and recessive germ-cells produced in the hybrid, but that they are produced *in equal numbers.* Of four ovules, two will be dominant and two recessive; and the same will hold true for the pollen grains.

But how will equal numbers of dominant and recessive germ-cells produce offspring in which the dominants exceed the recessives by three to one? For four individuals, we shall require four pollen grains and four ovules. Let us assume that a hybrid produces four ovules which are fertilized by four of its own pollen grains. What is *most* likely to happen, on the assumption that the dominant and recessive germ-cells exist in equal numbers, is shown by this diagram—Of the two dominant pollen grains-one will unite with a dominant ovule (*a*); the other with a recessive ovule (*b*); and of the two recessive pollen grains one will meet the remaining dominant ovule (*c*), and the other the recessive ovule (*d*). That is, all the possible combinations will occur. Other combinations than the above four might occur, and sometimes do so,—for instance, the pollen grain might unite with the second dominant ovule; but in the great majority of cases the result is as above stated, and so we get three individuals (*a*, *b*, and *c*) produced by at least one dominant germ-cell, and the result will be that they appear like the dominant parent; the fourth will be recessive.

Ovules. Pollen grains.



Germ-cells. Resulting individuals.

The result, you observe, is the same whether it be the pollen or the ovule that is dominant. It is, however, clear from the diagram that the three dominant offspring, though to all appearance quite similar, are yet differently constituted, for *a* is formed of two dominant germ-cells, whereas in *b* the pollen grain alone is dominant, and in *c* the ovule only is dominant.

a is a "pure dominant";
b and *c* are "impure dominants";
d is a "pure recessive."

Thus in the Fij generation we get, not three dominants to one recessive, but one pure dominant, two impure dominants, and one pure recessive. We must therefore amend the diagram on p. 11 thus—

```
        D × R
          |
        D[R] = Fj
          |
 _______________________
|       |       |       |
DD    D[R]    D[R]    RR = Fij
```

The former diagram shows their *appearance*—this shows their *Constitution.*

This is the usual result of the *self-fertilization* of hybrids of any contrasted pairs, and thus

in the Fij generation we get 3 talls to 1 dwarf,
3 coloured to 1 white,
3 smooth seeds to 1 wrinkled,
3 yellow seeds to 1 green.

When breeding is further continued we find that the pure dominant (DD) of Fij always breeds true, and produces—*e.g.* in case of stature, none but tall plants; the recessive (RR) produces none but dwarf plants; and the impure dominants (D[R]) produce the same kinds of offspring, and in the same proportions that the Fj generation produced, viz.—

1 DD, 2 D[R], and 1 RR.

The DD and D[R] plants *look* alike, and can only be distinguished by breeding. This being so, it follows that it is necessary for the horticulturist to keep the seeds of each of these plants separate if he wishes to find out which particular plant is the pure dominant. Hitherto it has been customary to mix the seeds of all individuals which appear alike, with the result that plants grown from them have shown various characters.

How is dominance accounted for? Messrs. **BATESON** and **PUNNETT** attribute it to the *presence* of some factor or ingredient, and the recessive character to its *absence*. Now, if recessives are marked by the absence of some factor, it follows that they can never reproduce the dominant character which depends for its manifestation upon the presence of this factor. A dwarf plant can never reproduce a tall, for tallness depends upon something which is absent from the dwarf. This has a most important bearing upon certain inherited diseases, for if the disease be dominant, owing to the presence of something, then the recessive individuals will not inherit it, and will not transmit it to their offspring.

Let us now summarize the **LAWS** that appear to me to have been established as regards a single pair of contrasted characters.

(1)	D × D	produces	DD.
(2)	R × R	,,	RR.
(3)	D × R	,,	D[R].
(4)	D[R] × R	,,	D[R] + R in equal numbers.
(5)	D[R] × D	,,	D[R] + D ,, ,,
(6)	D[R] × D[R]	,,	3 D + 1 R,
		or more correctly	1 DD + 2 D[R] + RR.

Law 4 may be shown to be true, thus—

PROFESSOR PUNNETT

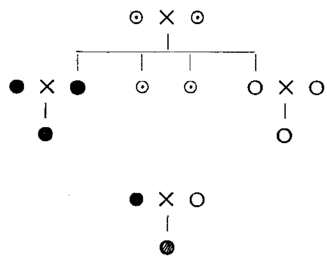
[*To face p.* 17.

D[R]		R		
●	×	○		●○
●	×	○	=	●○
○	×	○		○○
○	×	○		○○

Law 6 is illustrated in the self-fertilization of hybrids. These laws have been confirmed in several species of plants and animals.

I must now draw your attention to the fact that dominance is not invariably a feature of either member of a pair of contrasted characters. Sometimes the hybrid differs considerably from both parents. An exceedingly interesting example of this fact has been worked out by Prof. **Punnett.** He says, " Breeders have long recognized the difficulty of obtaining a pure breed of the Blue Andalusian Fowl. No matter how carefully the blues are selected, they always throw 'wasters' of two sorts, some pure *black*, and others of a peculiar *white* with black splashes. Careful breeding shows that, on an average, one *half* of the offspring from a pair of blue andalusians come blue, one *quarter* black, and one *quarter* white. These numbers at once suggest that the blues are hybrids" (see Law 6). " If this is so, it follows that the blacks and the splashed whites are pure, and ought to breed true. Experiment has shown that such is actually the case. Further, we should expect hybrid offspring from a union of the two pure breeds, the black and the white" (see Law 3). " Here, again, experimental results accord with theory. When a black and a white are bred together, all their offspring, without exception, are blue. The black and the white are pure-breeds, the so-called 'pure blue' is, and from its nature ever must be, a mongrel. The black and the white are two contrasted characters, and the essential feature of Mendel's theory, 'that the germ-cells remain pure in respect of each character,' could not be better shown."[1]

In the following diagram the black circles represent the black andalusians, the white circles the white birds, and the dotted ones the blue birds.



So far we have been considering Mendel's study of a single pair of contrasted characters, but he also observed the results of crossing plants which exhibited *two* pairs.

He called this "di-hybridism," or double-hybridism. For instance, he studied height and colour in the same hybrids by crossing a tall pea bearing coloured flowers with a dwarf white. Here you have two plants contrasted as to size and also as to the colour of the flowers. Of course the results are more complicated than when a single character only is dealt with. He found that each character acts independently, for tallness and colour are always dominant to dwarfness and absence of colour. You can therefore tell me what will be the result of—

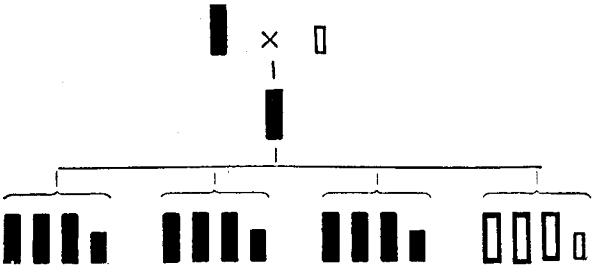
Tall coloured × Dwarf white.

The Fj generation will all be tall coloured.

The Fij generation will follow the result already established (Law 6) and consist of coloured plants and white in the proportion of 3 to 1, and talls to dwarfs in the proportion of 3 to 1. The smallest number of plants in

[1] The wording of the above quotation has been slightly altered so as to avoid technical terms.

Fij which will show all these results is 16, as illustrated in this diagram—



Here you observe 12 dark stripes representing the plants with coloured flowers, and 4 light stripes to represent the white ones. 12 to 4 is the 3 to 1 ratio. There are also 3 talls to every dwarf. So that we get

9 tall coloured,
3 dwarf coloured,
3 tall white,
1 dwarf white.

This ratio of 9·3·3·1 (9 with both dominant characters, 3 with only one such, 3 with the other, and 1 with both recessive characters) is true of any two pairs of contrasted characters.

I submit that a theory which will explain such a complicated result is most satisfactory. Mendelism—and so far Mendelism alone—has furnished the explanation.

I will now give you a problem to work out for yourselves. What will be the result of crossing wrinkled yellow seeds with smooth green if yellow is the dominant colour and smoothness the dominant surface ?—

WY × SG

The Fj generation will be—what ?—

SY (= smooth yellow)

Suppose a gardener ignorant of Mendelian laws wished to produce a wrinkled green pea as a new variety. Would he not at once say, after seeing the above result, "I have not only lost the wrinkled shape but I have lost the green colour as well; it is therefore of no use to continue the experiment"? But with Mendelism as a guide he now knows that he *must* get what he wants in the F_2 generation, which will consist of—what?—

SY	WY	SG	WG
(9)	(3)	(3)	(1)

And the gardener would know that the wrinkled green, being a pure recessive, must continue to breed true. He would thus have produced a new variety—and, please note he has obtained this result in the third year.

Some beautiful results have been obtained by Mr. Lock with Maize. Maize seeds are mostly yellow or white, and may be smooth or wrinkled. By crossing these we get

$$W \times W = W; \quad Y \times Y = Y; \quad Y \times W = Y.$$

This shows that Y is dominant to white. The F_1 yellow is a hybrid = D[R]. If it be crossed with W (Recessive) we ought, according to Law 4, to get yellow seeds and white seeds in about equal numbers. The actual numbers obtained by Lock were—

26751 white,
26792 yellow—

a very close approximation to theoretical requirements.

The yellow hybrid self-fertilized should produce

3 Y, 1 W.

Lock obtained

16705 yellow,
5568 white—($5568 \times 3 = 16704$).

Other results occurred as follows—

Smooth × Wrinkled
S
S W
5310 1765 (1765 × 3 = 5295).

Smooth yellow × Wrinkled white.
SY
SY WrY SWh WrWh
9 3 3 1

The Fj SY × WrWh (see Law 4)
SY WrY SW WrW
2869 2933 2798 2803

What is the inference from all these results? It seems abundantly evident that *plants and animals are built up of a number of indivisible unit factors upon which their characters depend*, and that these units are capable of acting independently of one another; *e.g.* in the maize seeds just referred to, the yellow, the white, the smooth and the wrinkled characters depend each upon a separate and quite independent factor. This is one of the most important conclusions to which we are led by Mendel's experiments.

"The fact," says Prof. Bateson, "that two cells are concerned in the production of all ordinary forms of life was discovered long ago, and has been part of the common stock of elementary knowledge of all educated persons for about half a century. The full consequences of this double nature seem to have struck nobody before Mendel. Simple though the fact is, to many it is difficult to assimilate as a working idea. We are accustomed to think of a man, a butterfly, or an apple-tree as each *one* thing. In order to understand the significance of Mendelism we must get thoroughly familiar with the fact that they are each *two* things, double throughout every part of their constitution. It is a good exercise to examine the people one meets with in daily life and to try, in a rough way, to analyze them into the two assemblages of characters which are united in them. That we *are* assemblages or medleys of our parental characteristics is obvious. We all know that a man may possess some of his father's features, whilst in other respects he resembles his mother. Now it is not generally seen that in each feature he is double. Yet it is obvious that the contribution of the male and female germ-cells may, in respect of any of the ingredients, be either the same or different. In any case in which the contributions made by the two cells is the same, the resulting individual is pure-bred for that ingredient; and in all respects in which the contribution from the two sides of the parentage is dissimilar, the resulting individual is cross-bred."

Thus every character of an individual (animal or plant) has a double origin.

What is the constitution of the germ-cells which any individual produces? "If both parent germ-cells brought a certain character in then all the daughter germ-cells will have it" (Law 1); "if neither brought it in, none of the daughter cells have it" (Law 2); "if it came in from one side and not from the other, then, on an average, in half the immediate descendants it will be present, and in the other half it will be absent" (Law 4; p. 17).

It follows that when a germ-cell transmits a certain quality, it transmits it as an undivided unit to another germ-cell—it transmits it undiluted, so that the resulting germ-cells either contain a full share of a certain quality, or none of it. That is, the quality is present or it is absent.

It also follows—and this is very important—that purity of type or breed has nothing to do with a prolonged course of selection or inheritance, as hitherto supposed. The black and the white andalusian fowls *born of blue mongrel parents* are just as "pure" as those which never had any "blue" ancestors.

There are some **Apparent Exceptions** to the rules I have enunciated; for instance, all white peas breed true, and only produce white flowers when self-fertilized. Most white crosses also breed true, but not invariably so. Prof. Bateson found that amongst the white peas called "Emily Henderson" the pollen grains are of two shapes, though only one kind is found in any particular flower. When he crossed these two kinds, there resulted, not white flowers, but *purple* ones only, in the Fj generation, and in the Fij generation 9 purples to 7 white in every 16.

White × White ["Emily Henderson"]

Purple

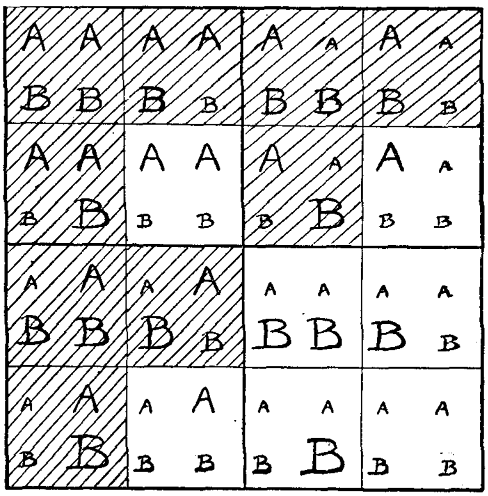
9 Purples　　7 Whites

Here we meet with what, at first sight, seems an exception to the rule. One might have expected 3 Purples to 1 White in the Fij generation (Law 6). But we are really dealing with a case of di-hybridism, in which the 9·3·3·1 numbers are changed to 9·7 by including the 3·3·1 in one form. The explanation is very ingenious, and throws a flood of light on what is known as "reversion to an ancestral type." This is perhaps the greatest difficulty which one encounters at the beginning of the study of Mendelism, but I will endeavour to clear up the difficulty. It is assumed that, in order to produce colour, *two* factors must be present. If one factor is present in one parent, and the other factor in the other parent, their mating will result in coloured offspring; the Fj generation will all be coloured because the two factors meet and combine. You might compare it to the action of one chemical upon another. I have in these two bottles[1] two different chemicals dissolved in a large proportion of water. They are both colourless, or nearly so.[2] You observe that on mixing them together a bright purple colour is produced. Something comparable to this probably occurs in the production of purple flowers from two white-flowered parents—*i.e.* two colourless substances combine, and their union produces colour.

Supposing this theory to be correct, the following diagram (borrowed from Mr. Punnett's *Mendelism*) will

(1) 4 plants where the A factor comes from both parents.

(2) 4 plants where A comes from one (male) parent only.



(3) 4 plants where A comes from the other (female) parent only.

(4) 4 plants where A is entirely absent.

help you to understand how it happens that in the Fij generation we get 9 coloured- to 7 white-flowered plants.

Let A represent one factor and B the other factor which must combine in order to produce colour, and small A and B their respective absence; then the diagram shows all the possible combinations of the A and B factors derived from the two parents in the 16 resulting individuals.

[1] Shown at lecture.

[2] One contained a few drops of perchloride of iron, and the other a few grains of salicylate of sodium.

There are 4 different A groups, each containing 4 plants.

All the possible arrangements of B [= BB Bb bB bb] are combined with each of the A groups.

Some of the squares are seen to contain both A and B; some contain A only; some B only, and one neither A nor B. Those which contain both A and B represent the coloured flowers, and there are 9 such; the other squares, of which there are 7, contain A only, or B only, or neither, and these represent the white flowers. You can, however, see that these 7 plants will differ in constitution, for 3 contain A only, 3 contain B only, and 1 contains neither A nor B; so that it is clearly an instance of the 9·3·3·1 ratio, though the last three kinds are identical in *appearance*. That these 7 *are* really different, and that some contain one factor and some the other factor, can be shown by mating them together; for those which contain A only, if mated with those which contain B only, will produce coloured offspring.

Two breeds of white rabbits have produced in the F_{i} generation all greys, and in the F_{ii} generation 9 greys, 3 blacks, and 4 whites.

This is another modification of the 9·3·3·1 ratio, which I must not stop now to explain.

A very striking result has been obtained by Prof. Bateson by mating a white Silky fowl with a white Breda. The offspring from this cross were all brightly coloured birds resembling the wild jungle fowl of India. These in the F_{ii} generation produced 9 coloured and 7 white.

Other experiments have been performed with rats, mice, pigeons, silk moths, snails, etc., and all without exception go to support Mendel's theory.

When scientists talk of such a subject as Mendelism, they are sometimes asked, "What is the use of it?" This question has been put to me. It is said that Benjamin Franklin was once asked a similar question, and he replied, "What is the use of a new-born baby?" The aim of the man of science is to gain knowledge of the world around him, to study Nature, and learn as much as he possibly can about its forces and phenomena, and he is not directly or immediately concerned with the application of these facts. Fortunately, I can give an answer which will be much more satisfactory to utilitarians than was Benjamin Franklin's.

For a great number of years agriculturists have been endeavouring to improve **British Wheat**. They have effected an immense number of crosses, without making any very substantial progress, because they have not had any guiding principle or theory to work upon. Now let us see what has recently been done by Prof. **Biffen** of Cambridge working on Mendelian lines. You are aware that certain kinds of wheat, including British wheat, are particularly liable to a disease which destroys the grain—a disease called "Rust." About £100,000,000 worth of wheat is destroyed annually.

On the other hand, there are some kinds—mostly small-eared wheats growing in America and elsewhere—which are not liable to this disease. They are immune.

It occurred to Mr. Biffen to cross these two kinds. The resulting hybrids were *all* affected by the disease, and so badly affected that he had difficulty in preserving any of the grains with which to continue the experiment. Now if you have quite understood what has gone before, you will at once see that he had achieved a great result, for this first experiment showed that the susceptibility to disease was a *dominant* character, and the immunity, or non-liability to disease, a recessive character. You can easily follow the further steps of the experiment, thus—

D × R
(susceptible) (immune)

D[R] (all affected)

DD D[R] D[R] RR

i. e. one quarter would be insusceptible. But this does not complete Biffen's results, for this large-eared grain was found dominant, as regards *size*, to the small-eared grain. So we have two dominant characters, viz. *Susceptibility to Rust* and *Large size*, contrasted with the two characters *Immunity* and *Small size*—a case of di-hybridism comparable to the tall coloured peas and the dwarf whites, and we can construct the Fij generation thus—

LR × SI

LR

9 LR 3 SR 3 LI 1 SI [1]

letting L = Large, R = Susceptibility to Rust, S = Small, and I = Immunity.

According to this there should be, in this Fij generation, about 3 large immune plants out of every 16; and these, being immune, will breed true. So that Biffen has transferred the immunity of the foreign wheat to what in other respects closely resembles the British variety. Last year there were several acres of this immune wheat growing on the experimental farm at Cambridge. Surely this is likely, from an economic and commercial point of view, to prove one of the most important experiments ever performed. He has also informed me that last year this corn yielded about 10 bushels per acre more than the ordinary British wheat.

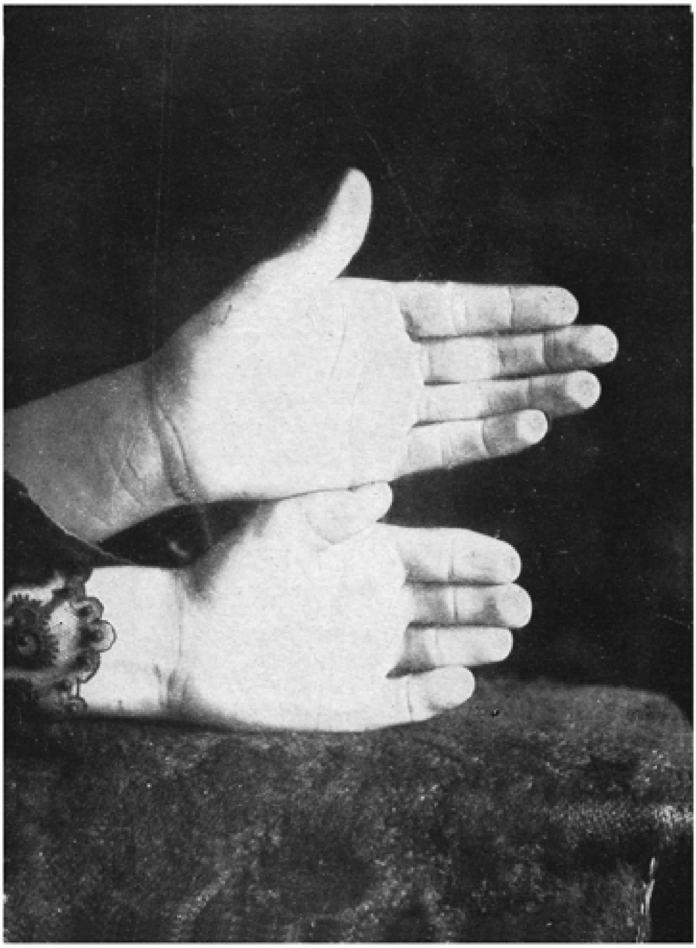
[1] This is what *would* almost certainly occur if these were only the factors named, but, as a matter of fact, the result was much more complicated.

I now come to the consideration of **Mendelism in Man.** Here the evidence of the action of Mendelian laws is scanty, but there has not been time for much investigation. The best example, so far, is that supplied by a family certain members of which are affected by a peculiar deformity of the hands and feet—technically termed "**Brachydactyly**," and consisting in the apparent absence of the middle bone of each finger and toe. The members of this family are divided into two classes: one class is quite normal, having ordinary hands and feet; the other class shows the apparent absence of the middle bone in every finger and toe (not reckoning the thumb and big toe). These abnormal individuals are also much below the average stature of their normal relatives.

This figure shows that the middle bone is present in the middle finger as a short cubical piece. It ought to be intermediate in length between the other two bones of the finger. The cubical piece at the base of the terminal bone of the other fingers is in reality the middle bone, which is ill-developed, and united into one with the terminal bone.

The middle bone of the foot is even more degenerate than the middle bone of the finger, and in each case it is found to form one piece with the terminal bone.

This abnormality has been hereditary through seven generations. It acts as a pure dominant. As each individual has had one abnormal parent, whilst the other parent was normal, they are impure dominants, or hybrids, so far as this anatomical feature is concerned, and can be represented by D[R]. Now when one of these abnormals marries a normal, *i. e.* a recessive, we get D[R] × R, and you know from Law 4 that one half of their children should show the abnormality, and the other half should be normal. Well, these abnormals have had 75 children, of whom 39 were abnormal, that is, 52 per cent.—a sufficiently close approxi-



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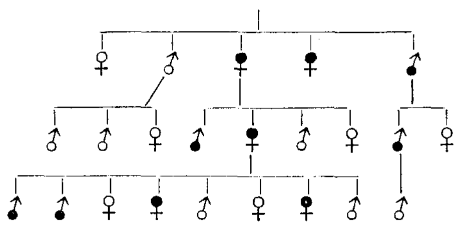
mation to the 50 per cent. required by theory. Moreover, you know the recessives breed true, and so we find it in this family, for the *normals* have not in a single instance transmitted this peculiar defect. Mr. Punnett refers to this family as exhibiting "the most conspicuous example of Mendelian heredity in man."

More recently Mr. Nettleship, a distinguished oculist, has published an account of a family affected by "congenital night-blindness" (an inability to see in a dim light). It has been hereditary through ten generations, and has been transmitted solely by the affected individuals. If we stop at the abnormal family in each line of descent, the proportion of affected to normals agrees almost exactly with Mendelian ratios.

Here is the chart of a family affected by spasmodic asthma, in which the numbers agree *exactly* with Mendel's law: 10 individuals suffered, whilst 10 were free from the disease (the descendants of the recessive must of course not be counted)—



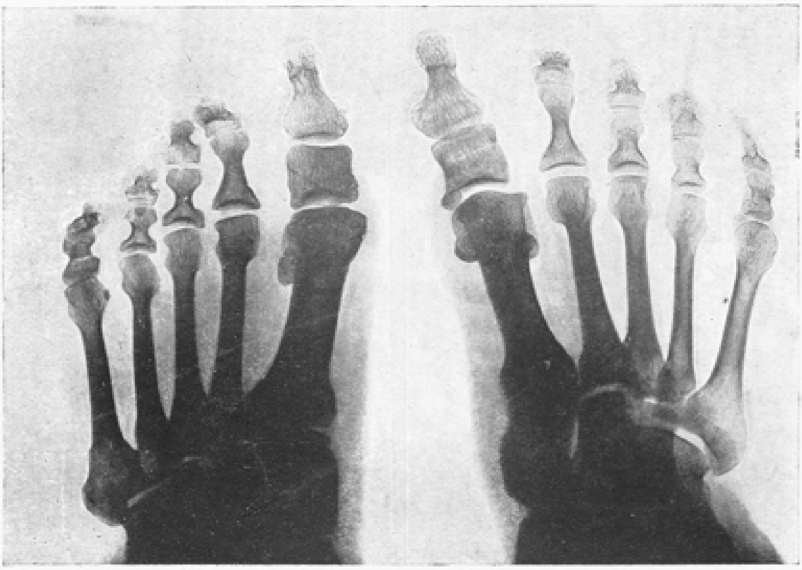
Spasmodic asthma. ● = 10 ○ = 10

There is a human disease called Hæmophilia, characterized by a tendency to bleed profusely from even slight wounds; as a rule the males alone suffer, and the females escape, but it is quite clear that, as an unaffected mother can transmit the disease to her male children, she herself must possess the disease in a latent form (as an impure dominant D[R] can transmit the recessive features.)

I have already referred to the opinion that living beings are essentially double in every character. This may be represented diagrammatically (see opposite page). Let A and B represent two germ-cells, which we will assume (for the sake of simplicity) to contain only 4 factors each (*a*, *b*, *c*, *d*, and *e*, *f*, *g*, *h*). Then C will represent the resulting individual. We see that it contains the two similar factors *a* and *e*, and is pure-bred for this quality. It is also pure-bred for the two bottom factors, but in respect of each of the other factors it is cross-bred, for it has only one dose of each. Suppose this individual to be a *man*, then he is fortunate if the top factors (black) are good qualities, and also if the bottom (white) factors represent defects which are absent. But what if *a* and *e* are bad qualities—a tendency to tuberculosis, mental defect, idleness, intemperance, or crime? How can an individual battle against such an inheritance? I leave you to think this out for yourselves.

Mendelism has thrown a great deal of light upon some hitherto obscure subjects, and, to say the least, it is a good working hypothesis.

I submit that the various facts that have been mentioned point out, with unmistakable clearness, the only way by which hereditary disease can be eliminated, and the kind of stock which should be produced. We hear now-a-days a great deal about physical deterioration, and much benefit is expected from education and from improved sanitary laws, but neither education nor sanitary laws can eradicate hereditary disease, *except by preventing the marriage of the affected individuals.* Just as a purely short-fingered race could be produced, so it would be equally easy to eradicate this abnormality by preventing the mating of the abnormal individuals, and there is little doubt that other hereditary diseases and defects can be made to practically disappear by the same means. Unfortunately modern legislation tends to produce the opposite effect, for everything is done



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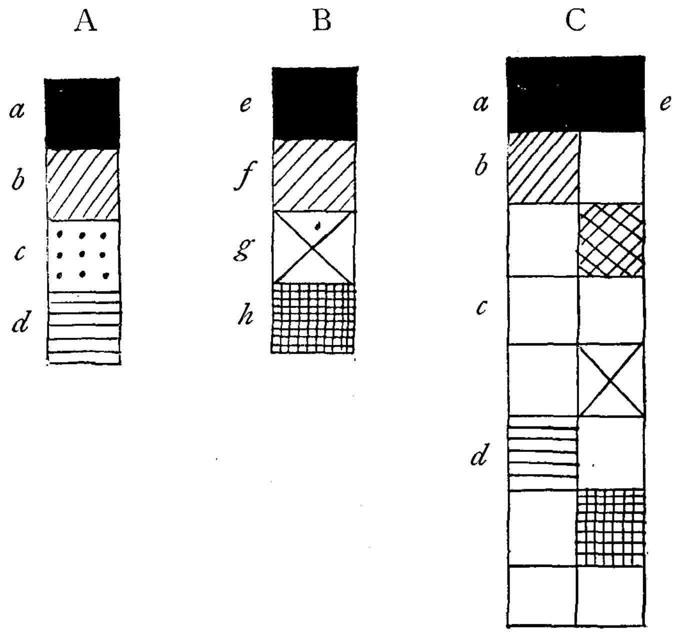
to encourage, not only the marriage, but the *early* marriage of inferior members of the community ; at the same time that the burdens of taxation retard more and more the



marriage of the middle and desirable classes. Free education, free meals, free clothing may be very well for a certain class, but *they are not remedies*, and the net result to this nation will, in the long run, be detrimental.

Had we but eyes to see, and ears to hear,
How perfect would this world appear !

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