CHAPTER I

MENDEL'S LAWS OF HEREDITY

IN 1857 an Austrian monk named Gregor Johann Mendel commenced a remarkable series of experiments in his cloister garden in the Abbey of Brünn. Interested in the problems of heredity and evolution, he began to experiment with the ordinary Garden Pea (*Pisum*). With a stroke of genius Mendel concentrated his experiments not only on one species of plant but on single characters in large numbers of individuals through several generations. The garden pea is a plant eminently suitable for this purpose, most of the races breeding true to type and many of the characters being distinct and discontinuous, that is to say, they do not grade into one another but are obviously different to the most casual observer. Moreover, as the plant is an annual, a generation can be raised in one year and large numbers can be raised in a small garden. Mendel selected seven pairs of the most distinct characters with which to work, and for illustration we will take one of these.

Most races of peas can be divided into two definite kinds, those with green and those with yellow seeds. Mendel first crossed a true-breeding yellow-seeded pea with pollen from a green-seeded pea and the result in the first generation (F_1) was all yellow-seeded peas (fig. 3). He then changed round and crossed a green pea with pollen from a yellow pea but the result was still the same, and in the first generation he obtained all yellow peas. He tried this experiment each way many times, always with the same result, pure yellow peas appeared every time in the first generation, and, although they had a green pea either for a father or a mother, no trace of the green parent could be found in the first crosses.

Mendel then sowed these cross-bred yellow peas and allowed them to self-fertilise. Each of the plants in the second generation (F_2) bore seeds of two colours, yellow or green, both colours often being found in the same pod (fig. 3). This proved that the cross-bred yellow peas contained the green factor although it was not patent, so Mendel called the yellow character *dominant* and the green character *recessive*. The next step was to sow the yellow and green peas of the second generation. Mendel sowed the green-coloured peas and found that they produced nothing but green peas in the third generation (F_3), and these being sown again gave

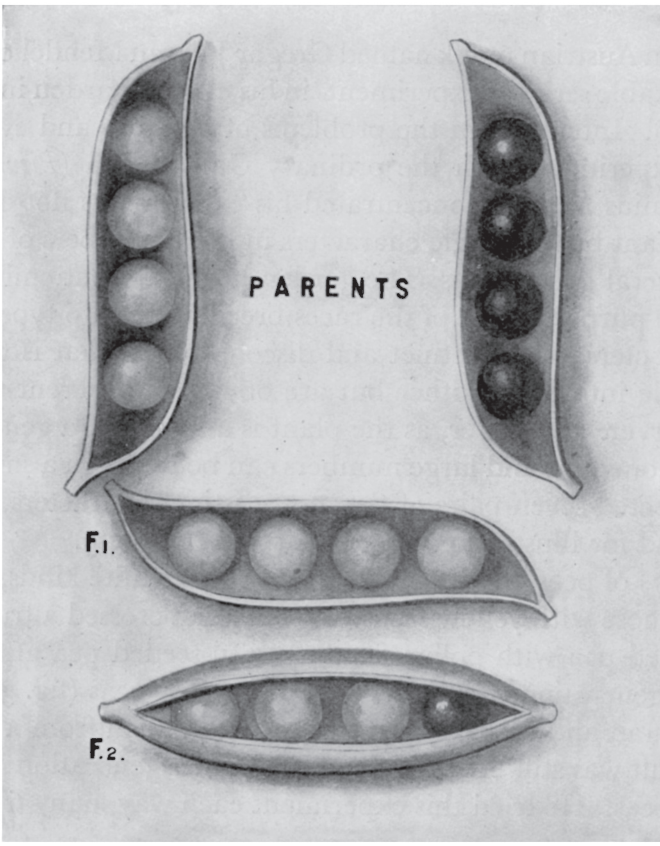

Fig. 3. The result of crossing Yellow (light-coloured) and Green (dark-coloured) Peas. In F_1 all yellow peas appear, in F_2 three yellows to one green. (After Morgan.)

nothing but green peas and so on for many succeeding generations ($F_4 ... F_n$). In a word, the green peas were "fixed" and always bred true with no throwing back to the yellow colour, notwithstanding that both parents and two grandparents were the dominant yellow. The yellow peas of the second generation, however, behaved very differently. When

Mendel sowed these he found that they were of two distinct kinds. Some were also "fixed" and bred quite true without throwing any greens but others threw a mixture of yellows and greens, just as the yellow peas from the original cross had done. He worked on for many generations with these peas and always found that while the greens and part of the yellows bred absolutely true the remainder of the yellows would always produce three kinds—pure yellows, pure greens and the impure yellows which would again give the same mixture. Throughout the experiments

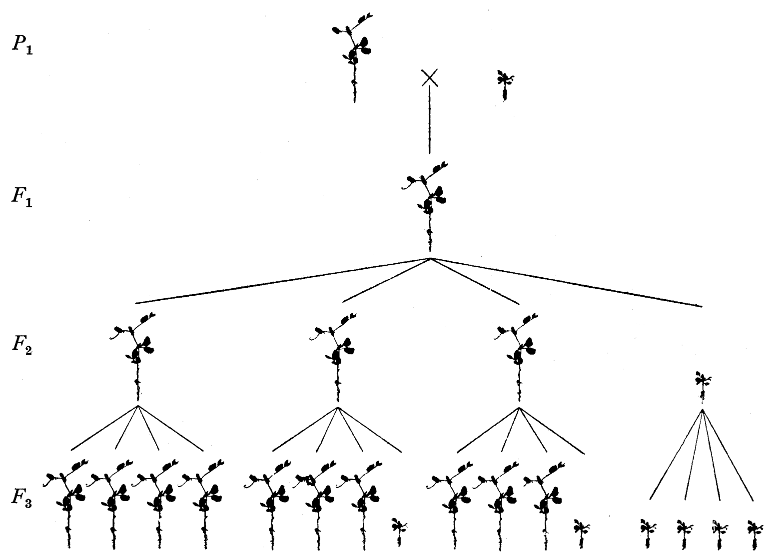

Fig. 4. The inheritance of tall and dwarf Peas. F_1 gives all tall (dominant), F_2 three talls to one dwarf. Of these in F_3 one tall breeds true, the other two throw talls and dwarfs in the ratio of 3 : 1, and the one dwarf breeds true. (After Darbishire.)

the pure yellow peas were quite indistinguishable from the impure yellows and their true nature could only be determined by their breeding behaviour. The purity of the extracted yellow dominants and the extracted green recessives was quite unexpected and forms the basis of what are now known as the Mendelian principles of heredity.

Another important and interesting fact that came to light during the experiments was that the three different types of peas always appeared in certain definite numerical proportions. On the average, out of every four peas there were one pure yellow, two impure yellows and one pure green, i.e. 25 per cent. pure yellow : 50 per cent. impure yellow : 25 per cent. pure green.

In Mendel's day it was known that at fertilisation an egg-cell of the female parent was joined by a pollen- or sperm-cell from the male parent, the union of these two forming the embryo from which the new individual arises. Mendel thus conceived the idea that these cells in some way bore the inherited characters, and that the yellow peas gave off germ-cells carrying the necessary factor to produce yellow, while the

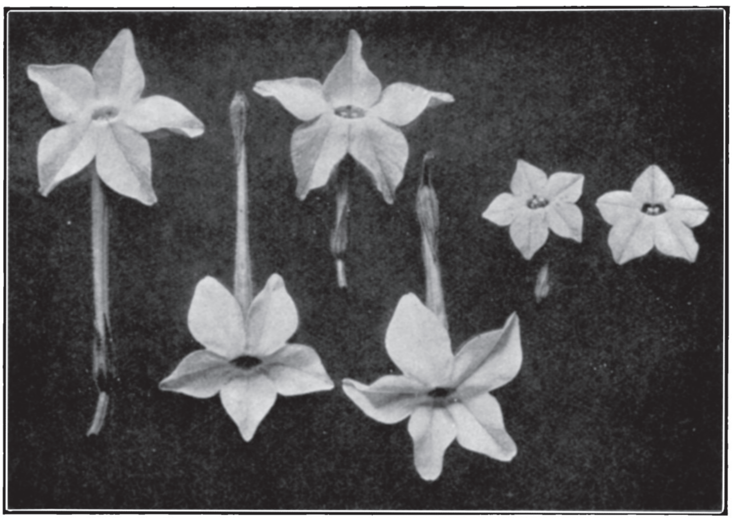

Fig. 5. Inheritance in the Tobacco Plant (*Nicotiana*). (Left) *N. alata grandiflora* with large flowers; (right) *N. Forgetiana* with small flowers; between, four flowers from the F_2 generation, showing the normal 3 : 1 ratio in the segregation of the characters, large and small flowers. (After Morgan.)

green peas carried the factor to produce green. When these two types of peas were crossed together the germ-cell from the yellow pea carrying the yellow factor met the germ-cell carrying green from the green pea and the two together formed an individual whose cells carried both yellow and green factors, but since in this case yellow is dominant to green, only yellow is visible in the first cross. The subsequent appearance of green peas in later generations proved that although it did not appear in the first cross the green factor still retained its identity and individuality, ready to appear at any time when by chance it became once more free of the dominating influence of the yellow factor. Mendel conceived that when the first cross formed its germ-cells these factors segregated, one-half of the germ-cells carrying green and one-half yellow. In normal chance fertilisations the green factor should become free from the dominating influence of the yellow on the average once in four times. Since the first cross, which carries equal numbers of pollen- and egg-cells bearing the yellow and green factors, is self-fertilised, yellow should meet green and green meet yellow in 50 per cent. of cases giving 50 per cent. impure yellows, while yellow should meet yellow in 25 per cent. of cases giving 25 per cent. pure yellows and green should meet green in 25 per cent. of cases giving 25 per cent. pure greens. The visible result therefore would be, on the average, 75 per cent. yellow and 25 per cent. green, or a ratio of 3 : 1 in the second generation (F_2). Mendel's actual experiments gave 6022 yellow and 2001 green seeds, or a ratio of 3·01 : 1. On repeating Mendel's original experiment the author obtained 1310 yellow and 445 green, or a ratio of 2·94 : 1. Other repeats by Correns, Tschermak, Bateson, Lock and Darbishire added to the above give a total of 134,707 yellow and 44,692 green, or a ratio of approximately 3·01 : 1.

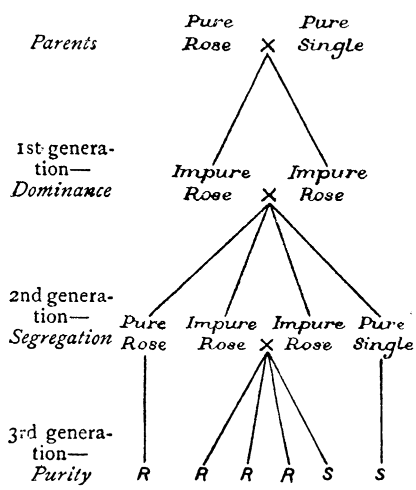

Fig. 6. Diagram showing the inheritance of Rose and Single Comb in Poultry.

The simple idea of the unity and purity of factors in the germ-cells, or gametic purity, is the most important of Mendel's discoveries and on it are founded all the complicated calculations of the probabilities of inheritance in different matings. This is known as the First Law of Mendel, the Law of Segregation of Germinal Units (now called "genes").

So far we have dealt with the inheritance of one pair of characters alone, now let us see what happens when more than one character pair is involved. Another difference between the seeds of garden peas is that

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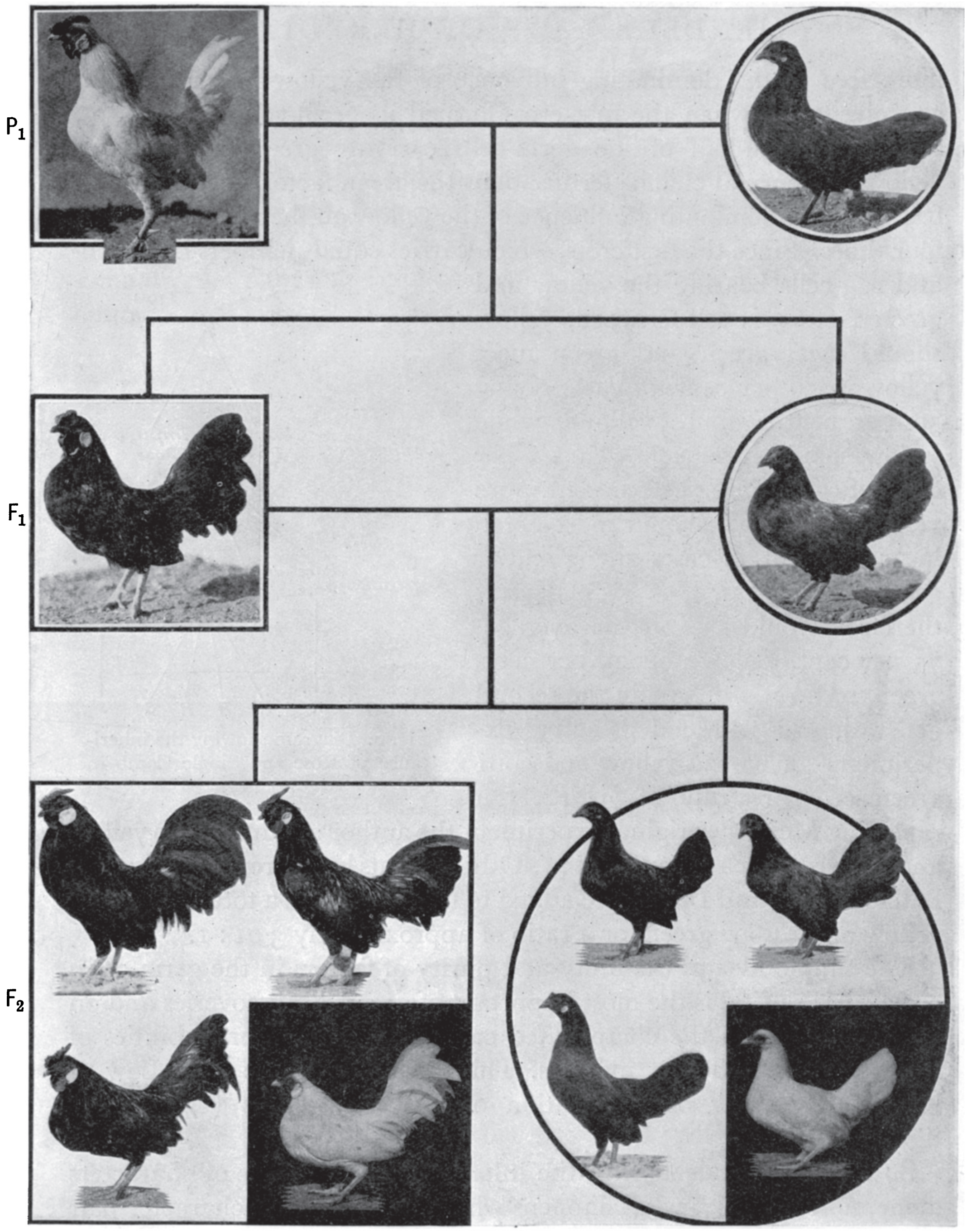
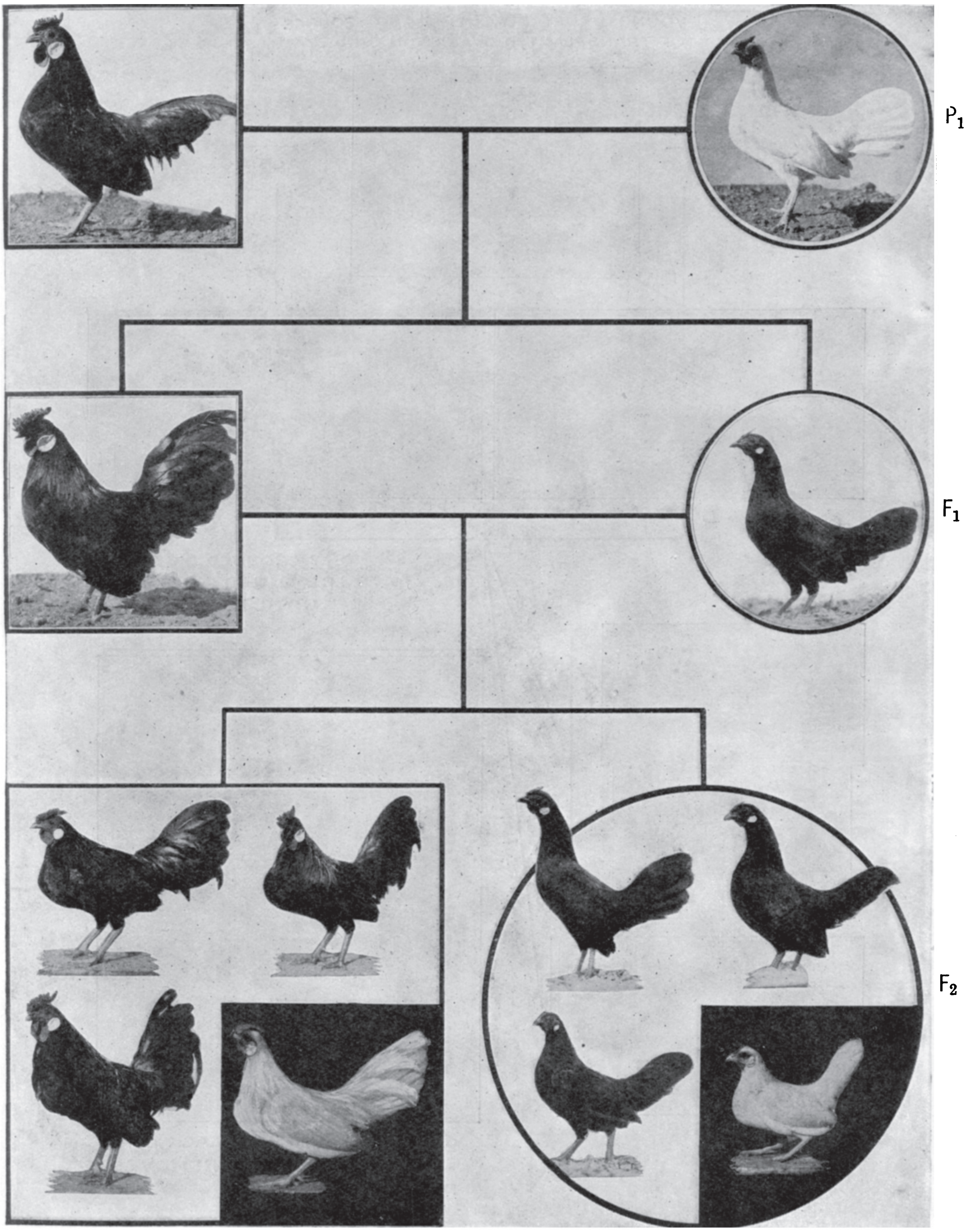


(*a*)

Fig. 7. Photographs of the progeny of a cross between recessive White Bantam cocks and dominant Black hens (*a*), and the reciprocal cross in which a Black cock is crossed with a White hen (*b*). In both cases the F_1 generation shows only black birds, whether cocks or hens, black being dominant



(*b*)

to white in Bantams, and in the F_2 we get three black birds to one white in both cocks and hens, thus showing that whichever way the cross is made there is no difference in the behaviour of the dominant character Black and the recessive White. (After Jull and Quinn, *Journal of Heredity*.)

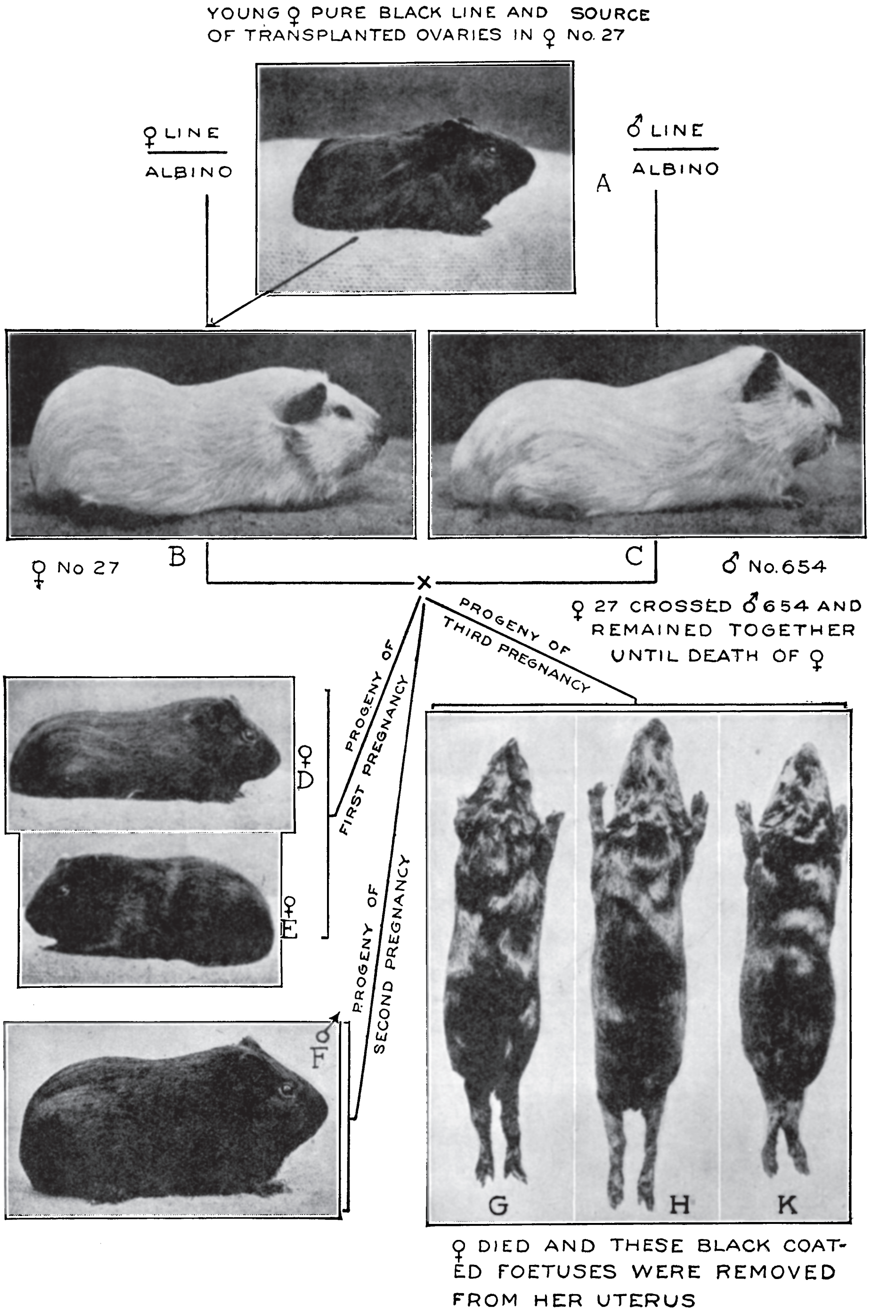


Fig. 8. Demonstration of the ability of the germ-cells to remain pure even in cases where they are nourished by unlike body-cells. Ovaries from a pure black guinea-pig were engrafted into a pure breeding albino which, on being mated with a pure albino male, produced only black offspring for three generations (until its death). (After Castle.)

in some races they are round and smooth while in others they are angular and wrinkled. We will now consider the crossing of a round yellow pea with a wrinkled green pea. In the first generation all the cross-bred seeds are round yellow, whichever way the cross is made, because, as Mendel found, the round and yellow characters are dominant to the corresponding wrinkled and green characters, which are recessive. In

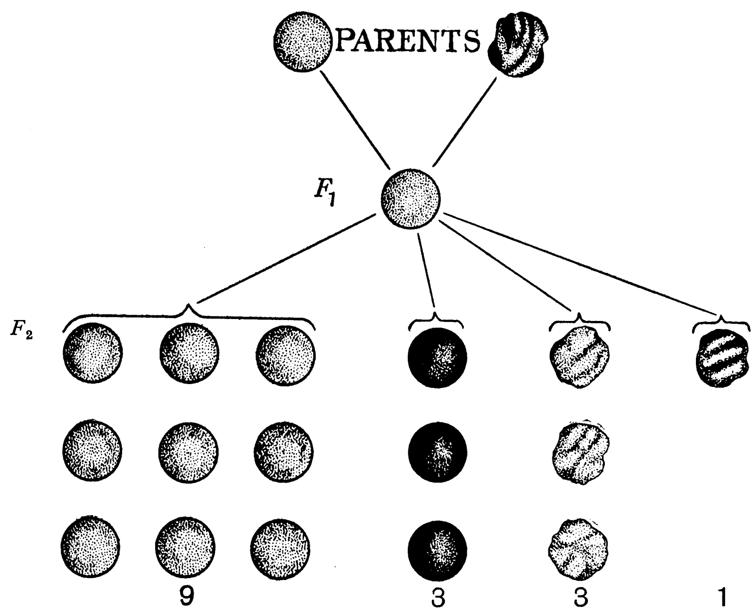


Fig. 9. The segregation of two distinct characters in Peas, round wrinkled and yellow green, showing in F_2 on the average, 9 round yellow, 3 round green, 3 wrinkled yellow and 1 wrinkled green. (Parents = round yellow × wrinkled green, F_1 = round yellow.) (After Morgan.)

the second generation these round yellow cross-breds self-fertilised produce on the average a proportion of 3 round to 1 wrinkled and 3 yellow to 1 green. Taking the two characters in combination, there are, in every 16 peas, on the average 9 round yellow, 3 round green, 3 wrinkled yellow and 1 wrinkled green or $(3\,R:1\,W) \times (3\,Y:1\,G) = 9\,RY:3\,RG:3\,WY:1\,WG$. Fig. 9 and the following table will explain this more clearly.

Here we see that the round yellow-seeded first cross has four kinds of germ-cells, those carrying factors for round and yellow, those carrying

Egg-cells of the Round Yellow Cross

Pollen-cells of the Round Yellow Cross	*RY*	*WY*	*RG*	*WG*
RY	*RY* *RY* round yellow (pure)	*WY* *RY* round yellow	*RG* *RY* round yellow	*WG* *RY* round yellow
WY	*RY* *WY* round yellow	*WY* *WY* wrinkled yellow (pure)	*RG* *WY* round yellow	*WG* *WY* wrinkled yellow
RG	*RY* *RG* round yellow	*WY* *RG* round yellow	*RG* *RG* round green (pure)	*WG* *RG* round green
WG	*RY* *WG* round yellow	*WY* *WG* wrinkled yellow	*RG* *WG* round green	*WG* *WG* wrinkled green (pure)

wrinkled and yellow, those carrying round and green and those carrying wrinkled and green. These four kinds occur in approximately equal numbers both in the pollen- and in the egg-cells. Since yellow and round are dominant to green and wrinkled respectively, the resulting individual shows the dominant characters only, and out of sixteen individuals only one is free of both the yellow and the round factors, i.e. a double recessive which will be wrinkled green. With regard to the others, of the three wrinkled yellow seeds one breeds true, which carries only wrinkled and yellow with no round or green. The other two split up again into wrinkled yellow and wrinkled green. Of the three round green peas one alone breeds true—that which carries only the round and green, the other two split up again into round green and wrinkled green. The nine round yellow peas are more complicated still. Only one—that carrying only round and yellow—breeds true. Of the others, two throw round yellows and wrinkled yellows, two throw round yellows and round greens, while the remaining four are like the original cross-bred and produce 9 *RY* : 3 *RG* : 3 *WY* : 1 *WG*. In Mendel's experiments the actual numbers were 315 *RY* : 108 *RG* : 101 *WY* : 32 *WG*. In the author's repeat experiments the numbers were 997 *RY* : 338 *RG* : 313 *WY* : 107 *WG*. In 1905 the *RY* seeds of one of the F_3 plants of this experiment were sent to the late Mr A. D. Darbishire, who continued