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Heredity and Development, SECOND EDITION

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Mendelism

During the entire period from Darwin's attempted synthesis of the facts of inheritance down to 1900, a scientific paper that was to revolutionize our understanding of heredity lay unappreciated on the shelves of many libraries. The article itself had been published in 1866. In it the author, Gregor Mendel, presented some of the results of his experiments in crossing varieties of garden peas.

The Discovery of Mendel's Paper. The 'discovery' and appreciation of the importance of Mendel's paper is a very dramatic incident in the history of science. Three individuals in the year 1900 realized the great importance of Mendel's work.

During the 1890s there had been renewed interest in plant hybridization. The three scientists who 'discovered' Mendel—Hugo de Vries, Carl Correns, and Erik von Tschermak—were doing breeding experiments of their own. Each of them independently came to more or less the same conclusions that Mendel had expressed in 1866 *before they knew of Mendel's paper*. This is another example of a frequent happening in science. When the field is 'ready,' the discovery is certain to be made. If Mendel had never lived, the history of genetics would not have been greatly different. About the year 1900, either

he would be rediscovered or, had he never lived, others would reach essentially the same conclusions as he had in 1866. His work was unappreciated in his own lifetime, for biologists in 1866 had neither the background nor the prescience to understand the significance of what he had accomplished.

Gregor Mendel's famous article is not a scientific paper in the usual sense, but a lecture presented to the Natural History Society of Brunn in 1865. The full results of his research were never published, but the portion that he did include, coupled with an extraordinary analysis of the data, makes his paper one of the landmarks of science.

Mendel was fully aware that experiments in plant breeding had been conducted by many famous men. It was true, nevertheless, that no general principles had emerged from previous studies. To Mendel this was a serious affair, since an understanding of inheritance was essential for an understanding of evolution and he was deeply interested in Darwin's work (*The Origin of Species* appeared during the period he was conducting his experiments). He began experiments that were intended to give information on inheritance and evolution.

Peas as Experimental Material. Mendel selected peas for his experiments because they possessed many desirable features:

1. Numerous varieties of peas were available commercially. They provided the material that he studied.
2. The plants were easy to cultivate and the generation time was short.
3. The offspring of the crosses between the varieties were fertile.
4. The structure of the pea flower is such that accidental pollination was thought not to occur. The anthers that produce the pollen and the stigma where the pollen grains germinate are completely enclosed by the petals. Normally, pollen from a flower falls on the stigma of the same flower and self-fertilization results. In those cases where crosses between varieties are desired, it is possible to remove the anthers before they mature and somewhat later, when the stigma is mature, to cover it with pollen from another flower.

Mendel's approach to the problem of inheritance was different from that of previous workers. His predecessors had concentrated on the whole organism. Usually they had crossed varieties that differed in many characters and the offspring were found to be intermediate or in rare cases more like one parent. Mendel focused his attention on specific differences and studied how these were inherited generation after generation. Some of his varieties had *round* seeds; others had *wrinkled* seeds. In all he studied seven different characters of the pea, and for each he had two varieties, as shown in the following lists:

CHARACTER AFFECTED	VARIETIES
Seed shape	<i>round</i> or <i>wrinkled</i>
Seed color	<i>yellow</i> or <i>green</i>
Seed coat color	<i>colored</i> or <i>white</i>
Pod shape	<i>inflated</i> or <i>wrinkled</i>
Pod color	<i>green</i> or <i>yellow</i>
Flower position	<i>axial</i> or <i>terminal</i>

Stem length

long or short

Crosses of Plants with Contrasting Characters. First, he made sure that all of his varieties would breed true. Once this was established he made crosses between all of the pairs just listed. The results were most unexpected in the light of earlier experiments by other plant breeders: the offspring were never intermediate but were always like one of the parents. When peas with *round* seeds were crossed with peas with *wrinkled* seeds, for example, the offspring were plants with *round* seeds. Mendel spoke of the form that appeared in the offspring as *dominant* in comparison to the form that did not appear, which he called *recessive*. Dominance can be determined only by making a cross and observing the type of offspring obtained; it could not be predicted before the experiment was performed merely by examining the parent plants. The varieties that Mendel used were found to have these relationships:

DOMINANT	RECESSIVE
<i>round</i> seed	<i>wrinkled</i> seed
<i>yellow</i> seed	<i>green</i> seed
<i>colored</i> seed coat	<i>white</i> seed coat
<i>inflated</i> pod	<i>wrinkled</i> pod
<i>green</i> pod	<i>yellow</i> pod
<i>axial</i> flowers	<i>terminal</i> flowers
<i>long</i> stem	<i>short</i> stem

Over the course of years, geneticists have introduced some terms that make it easier to discuss crosses. The original parental generation is abbreviated P. The offspring of the P generation is the first filial or F₁ generation. The offspring of the F₁ is the second filial generation or F₂, the third is the F₃, and so on. It is also customary to describe crosses in terms of the character. Thus, the cross of a plant with round seeds with a plant with wrinkled seeds is shortened to *round*×*wrinkled*.

The F₂ Generation. Some plant breeders might have stopped the experiments after a single cross had determined dominant and recessive characteristics. The results were clear cut. The F₁ plants were always like one of the parents. Mendel, however, continued his crosses and was careful to realize that although an F₁ of the *round*×*wrinkled* might be identical with the *round* parent, its parentage was different. Perhaps its offspring would reflect the different origin.

Since peas are self-fertilizing, the F₁ plants pollinated their own ovules and gave the F₂, and when Mendel studied the F₂ plants he found that both dominant and recessive characters were present. Now he did a simple though revolutionary thing: he counted the number of individuals of each type. In every cross there was a ratio of 3 dominant to 1 recessive. His results can be summarized as follows:

P	F ₁	F ₂	COUNTS	RATIO
<i>round</i> × <i>wrinkled</i>	<i>round</i>	5,474	<i>round</i>	2.96:1
		1,850	<i>wrinkled</i>	
<i>yellow</i> × <i>green</i>	<i>yellow</i>	6,022	<i>yellow</i>	3.01:1
		2,001	<i>green</i>	
<i>colored</i> × <i>white</i>	<i>colored</i>	705	<i>colored</i>	3.15:1
		224	<i>white</i>	
<i>inflated</i> × <i>wrinkled</i>	<i>inflated</i>	882	<i>inflated</i>	2.95:1
		299	<i>wrinkled</i>	

<i>green pods</i> × <i>yellow pods</i>	<i>green</i>	428	<i>green</i>	
		152	<i>yellow</i>	2.82:1
<i>axial</i> × <i>terminal</i>	<i>axial</i>	651	<i>axial</i>	
		207	<i>terminal</i>	3.14:1
<i>long</i> × <i>short</i>	<i>long</i>	787	<i>long</i>	
		277	<i>short</i>	2.84:1

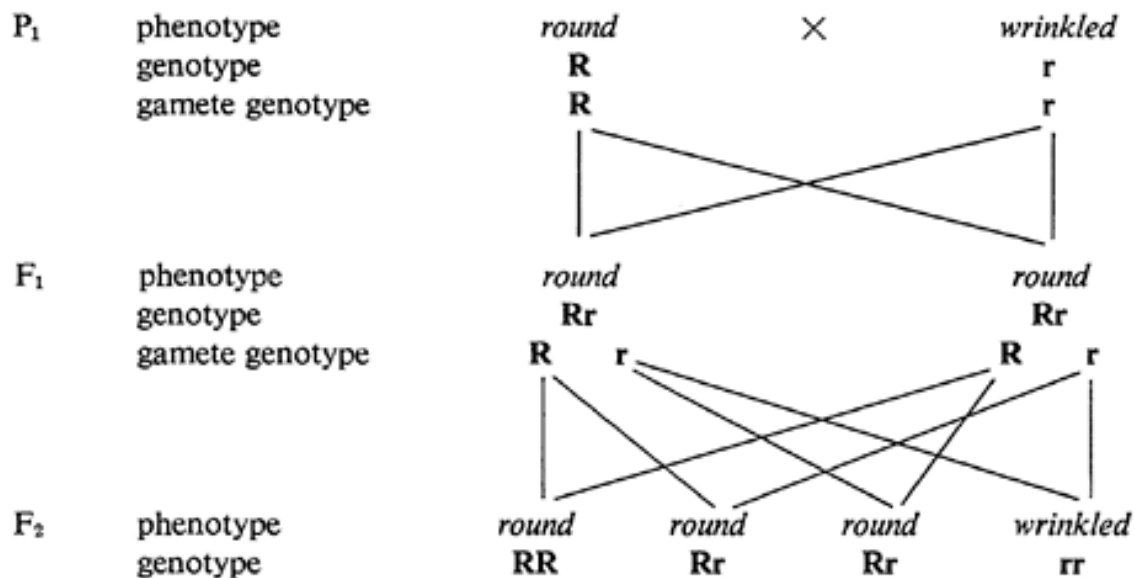
These results would suggest that the rules of inheritance were the same, irrespective of the varieties being crossed. The F_1 plants were always of one type, which resembled one of the parents. In the F_2 , two classes appeared and the frequency was 75 per cent dominants and 25 per cent recessives, or a ratio of 3:1.

The F_3 Generation. Mendel continued his experiments and obtained an F_3 generation.

We may take as an example the *round*×*wrinkled* cross, which in the F_2 gave 75 per cent *round* and 25 per cent *wrinkled*. He allowed a number of the *wrinkled* plants to self-fertilize to give an F_3 , and found that all bred true, that is, only *wrinkled* plants were obtained in the F_3 . The F_2 *round* plants gave two results:

1. One-third (193 of 565 plants) bred true, giving *round* plants in the F_3 .
2. Two-thirds (372 of 565 plants) gave *round* and *wrinkled* in a ratio of 3:1. On the basis of their genetic behavior these were like the F_1 plants.

Mendel's Hypothesis. Mendel explained these results in this way: Let us assume that the *round* variety is round because it has a gene **R**, and the *wrinkled* variety is wrinkled because it has gene **r**. (Mendel did not use the term gene but spoke of 'factors' or 'traits.' It will be simpler for us to use the modern term gene from the very beginning and note the gradual change in its meaning. For the present we shall understand a gene to be the basis of an inherited character. We will not commit our-selves further to what it is or where it is.) If a cross is made between the *round* and *wrinkled* varieties, the gametes of the *round* plant will have **R** and the gametes of the *wrinkled* plant will have **r**. Fertilization will produce an F_1 with both genes, **Rr**. In appearance this plant is *round*, **R** being dominant and **r** recessive. We speak of the appearance of the individual as its *phenotype* and the genetic composition of the individual as its *genotype*. Thus, the phenotype of this F_1 plant is *round* and its genotype is **Rr**. Plants of the **Rr** type will produce gametes and Mendel assumed that any single gamete would contain either **R** or **r** but never both. He also assumed that gametes containing **R** and gametes containing **r** are produced in equal numbers. If the union of F_1 gametes is at random, then we will obtain a 3:1 ratio of *round* to *wrinkled*. The entire cross could be presented in this schematic manner:



It is actually unnecessary to show two plants in the F_1 since both are the same. Two are used in order to make it easier to visualize the cross that gives the F_2 .

This scheme provides a formal explanation of the results, namely, the origin of the 3:1 ratio. It also shows that the F_2 *round* plants are of two types. One in three of the *round* plants is pure *round*. If self-fertilized, it would breed true. The remaining 2/3 of the *round* plants are **Rr**. If these are allowed to self-fertilize there will result an F_3 ratio of 3 *round* to 1 *wrinkled*. It will be recalled that Mendel made these tests of the F_2 and the theoretical and actual results are the same.

This schematic interpretation applies to all of Mendel's crosses involving one pair of genes. Several important conclusions can be reached if the interpretation is correct:

1. Dominant and recessive genes do not affect one another. In the F_1 of the cross discussed, the genotype was **Rr**. There was no visible effect of the **r** gene, the seeds being just as round as in the pure *round* parent. When the **Rr** plant was allowed to self-fertilize both *round* and *wrinkled* seeds were obtained. These F_2 *wrinkled* seeds were identical in appearance to the P generation *wrinkled* seeds.
2. The gametes produced by an F_1 plant of the **Rr** constitution will contain either **R** or **r**, never both.
3. The **R** and **r** types of gametes will be produced in equal numbers by an **Rr** plant.
4. Combination between gametes is a chance affair, and the frequency of different classes of offspring will depend on the frequencies of gametes. Since an F_1 plant having the **Rr** constitution will produce 50 per cent gametes of the **R** type and 50 per cent gametes of the **r** type, the mathematical basis of the F_2 frequencies will be as follows:

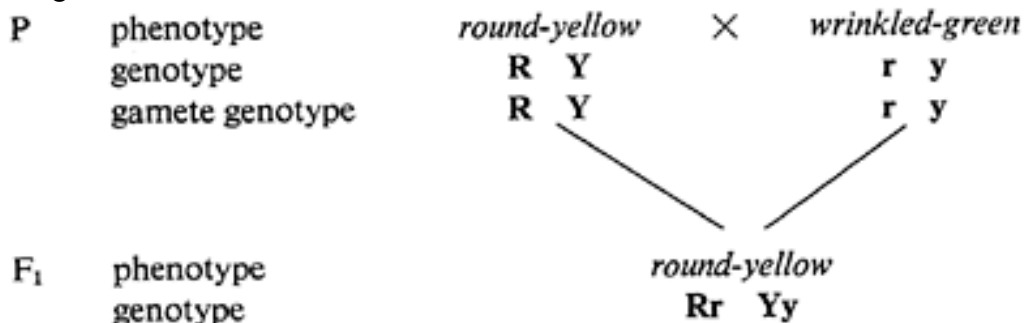
		POLLEN	
		50% R	50% r
OVULES	50% R	25% RR	25% Rr
	50% r	25% Rr	25% rr

Crosses Involving Two Pairs of Genes. Mendel's next step was to see if the conceptual scheme devised for crosses involving one pair of genes could be applied to crosses involving two pairs of genes. For this he used *round* and *wrinkled* as one pair and *yellow* and *green* as the other. Previous work had shown that the cross between *yellow* and *green* produced *yellow* in the F_1 and a ratio of 3 *yellow* to 1 *green* in the F_2 .

When a cross was made between a plant with *round-yellow* seeds and a plant with *wrinkled-green* seeds all of the F_1 plants had *round-yellow* seeds. In the F_2 the following seed types were obtained:

315	<i>round-yellow</i>
108	<i>round-green</i>
101	<i>wrinkled-yellow</i>
32	<i>wrinkled-green</i>

One interesting thing brought out by these data is the appearance of two new seed types that were not present in either the P or the F_1 generation. These new types are *round-green* and *wrinkled-yellow*. This and the other results, however, fit perfectly into the Mendelian scheme, if we assume the complete independence in inheritance of the two pairs of genes. The cross would be as follows:



In the formation of gametes by the F_1 plant, Mendel assumed that a gamete would have only one member of a pair of genes. Thus, a gamete would have either **R** or **r** and in addition either **Y** or **y**. Four classes of gametes would be produced and these in equal frequency. The classes would be **RY**, **Ry**, **rY**, and **ry**. If an F_1 plant is allowed to self-

fertilize there will be these four types of pollen and the same four types of ovules. This will give 16 possible combinations, as shown below:

		POLLEN			
		RY	Ry	rY	ry
OVULES	RY	RR YY <i>round-yellow</i>	RR Yy <i>round-yellow</i>	Rr YY <i>round-yellow</i>	Rr Yy <i>round-yellow</i>
	Ry	RR Yy <i>round-yellow</i>	RR yy <i>round-green</i>	Rr Yy <i>round-yellow</i>	Rr yy <i>round-green</i>
	rY	Rr YY <i>round-yellow</i>	Rr Yy <i>round-yellow</i>	rr YY <i>wrinkled-yellow</i>	rr Yy <i>wrinkled-yellow</i>
	ry	Rr Yy <i>round-yellow</i>	Rr yy <i>round-green</i>	rr Yy <i>wrinkled-yellow</i>	rr yy <i>wrinkled-green</i>

Of the 16 possible F_2 combinations, 9 will be *round-yellow*, 3 will be *round-green*, 3 will be *wrinkled-yellow*, and 1 will be *wrinkled-green*. Here is a comparison of Mendel's data with the theoretical expectation:

	ACTUAL	EXPECTED
<i>Round-yellow</i>	315	313
<i>Round-green</i>	108	104
<i>Wrinkled-yellow</i>	101	104
<i>Wrinkled-green</i>	32	35
	556	556

The figures given in the 'actual' column are those obtained by counting the seeds. The 'expected' values are computed in this manner: If we have a total of 556 plants and expect 1/16 of them to be *wrinkled-green*, we find 1/16 of 556, which is 35. The other expected classes are 9/16, 3/16, and 3/16 of 556.

Testing the Hypothesis. Mendel made a further test of the adequacy of his hypothesis. He predicted that the F_2 plants would have four phenotypic classes and a total of nine genotypic classes (refer to the checkerboard). Genetic tests would allow him to distinguish among plants of the same phenotype but of different genotypes. His test consisted of allowing all the F_2 plants to self-fertilize to produce an F_3 and then seeing if the actual results of the crosses were the same as were expected on the basis of the hypothesis. This is what he found. *The Breeding Behavior of the F_2 Round-yellow.* It can be seen from the checkerboard that 9/16 of the F_2 plants are *round-yellow*. These plants are listed in the first column of the table that follows, grouped according to genotype. These plants are all of the same phenotype but they belong to four different genotypes, namely **RRYY**, **RRYy**, **RrYY**, and **RrYy**. Although of identical appearance, these four genotypes should be distinguishable on the basis of the ratios of the types of offspring they will produce following self-fertilization. These predicted ratios are listed in the third

column. The fourth column gives the number of plants that one would expect to give the ratio listed in column 3, if Mendel's hypothesis is correct. For example, Mendel predicted one out of every nine *round-yellow* plants to be **RRYY**. If a plant of this genotype is self-fertilized, it would give only *round-yellow* offspring in the F_3 . No other genotype will give this result. Mendel planted 315 of the F_2 *round-yellow* plants and of these 301 gave progeny. He would predict therefore 1/9 of these 301 plants, or 33, to be **RRYY** and give only *round-yellow* seeds. The fifth column gives the actual results. In the example we have been using, Mendel predicted that 33 of the plants would be **RRYY** and he found that 38 were of this genotype.

F_2	FREQUENCY	EXPECTED F_3 RATIOS	NUMBER EXPECTED	ACTUAL NUMBER
RRYY	1/9	all <i>round-yellow</i>	33	38
Y				
RRYy				
y				
RRYy	2/9	3 <i>round-yellow</i> ; 1 <i>round-green</i>	67	65
y				
RrYY				
Y				
RrYY	2/9	3 <i>round-yellow</i> ; 1 <i>wrinkled-yellow</i>	67	60
Y				
RrYy				
RrYy				
RrYy	4/9	9 <i>round-yellow</i> ; 3 <i>round-green</i> ; 3 <i>wrinkled-yellow</i> ; 1 <i>wrinkled-green</i>	134	138
RrYy				

301 301

The Breeding Behavior of the F_2 Round-green. Three-sixteenths of the F_2 were of this category. Mendel raised 102 of these plants and these are the results:

F_2	FREQUENCY	EXPECTED F_3 RATIOS	NUMBER EXPECTED	ACTUAL NUMBER
RRyy	1/3	all <i>round-green</i>	34	35
y				
Rryy				
Rryy	2/3	3 <i>round-green</i> ; 1 <i>wrinkled-green</i>	68	67

102 102

The Breeding Behavior of the F_2 Wrinkled-yellow. The *wrinkled-yellow* comprised 3/16 of the F_2 . Mendel raised 96 of these plants and these are the results:

F_2	FREQUENCY	EXPECTED F_3 RATIOS	NUMBER EXPECTED	ACTUAL NUMBER
rrYY	1/3	all <i>wrinkled-yellow</i>	32	28
Y				
rrYy				
y				
rrYy	2/3	3 <i>wrinkled-yellow</i> ; 1 <i>wrinkled-green</i>	64	68
y				
			96	96

The Breeding Behavior of the F₂ Wrinkled-green. This category comprised 1/16 of the F₂. Mendel raised 30 plants of this type. The results were as follows:

F ₂	FREQUENCY	EXPECTED F ₃ RATIOS	NUMBER EXPECTED	ACTUAL NUMBER
rryy	1	all wrinkled-green	30	30

The fact that the F₂ plants gave an F₃ that did not differ materially from the prediction, indicated that Mendel's conceptual scheme of inheritance was in full accord with his experimental results. In every case the actual values are surprisingly close to those expected. The expected values are based on the probability of the various types of gametes combining in a certain way. The expected and actual values are rarely identical: we should not expect them to be so any more than we should always expect five heads for every ten tosses of a coin.

Mendel went one step farther and crossed plants differing in three contrasting characters. The results were entirely according to expectation but they will not be discussed.

These are some of the conclusions that may be drawn from Mendel's experiments:

1. The most important conclusion is that inheritance appears to follow definite and rather simple rules. Mendel was able to apply the same type of explanation to the results of all of his crosses. He had reached that stage in the development of a scientific theory where results could be predicted with a high degree of accuracy. This is one goal of a scientist.
2. When plants of two different types were crossed, there was no blending of the individual characteristics. Mendel studied seven pairs of contrasting characters. One member of each pair of contrasting characters could be thought of as dominant and the other as recessive. In a hybrid formed from crossing a pure-breeding dominant and a pure-breeding recessive, the appearance of the plant was identical with that of the dominant parent.
3. The factors responsible for the dominant and recessive condition were not modified by their occurrence together in a hybrid. If two hybrids were crossed, both dominant and recessive offspring would appear. Neither the dominant nor the recessive offspring would give any evidence of contamination resulting from hybridization. In short, an F₂ recessive would be identical in genotype and phenotype to the P generation recessive.
4. When a pure-breeding plant exhibiting a dominant characteristic (**A**) is crossed with a recessive (**a**) the F₁ (**Aa**) is like the **A** plant in appearance. *Segregation* occurs in the F₂, which results in a ratio of three plants having the dominant character (one of which will be pure breeding and the other two like the F₁) to one recessive. Segregation is often called *Mendel's First Law*.

5. If two pairs of genes, such as **Aa** and **Bb**, are involved in a cross, each pair acts independently so far as transmission to the next generation is concerned. This phenomenon is known as *independent assortment* and it is often spoken of as *Mendel's Second Law*. Its mode of operation can be understood if we consider the F_2 originating from an F_1 **AaBb** plant. So far as the phenotypes are concerned 3/4 of the F_2 will have the **A** phenotype and 1/4 will have the **a** phenotype. The same is true for the other pair of genes: 3/4 of the plants will have the **B** phenotype and 1/4 will have the **b** phenotype. It is entirely a matter of chance which combination of genes a given F_2 plant will receive. Thus of the 3/4 that will have the **A** phenotype, 3/4 will also have the **B** phenotype and 1/4 will have the **b** phenotype. Of the 1/4 that will have the **a** phenotype, 3/4 will have the **B** phenotype and 1/4 will have the **b** phenotype. So far as both characters are concerned 9/16 of the F_2 (3/4 of 3/4) will have both the **A** and **B** phenotypes, 3/16 will have the **A** and **b** phenotypes, 3/16 will have the **a** and **B** phenotypes, and 1/16 will have the **a** and **b** phenotypes. The 9:3:3:1 ratio of the F_2 is due to the independent assortment of genes in the gametes of the F_1 plant.
6. The gametes will contain only one type of inherited factor of each contrasting pair. Thus the gametes of an F_1 **Aa** plant will produce gametes containing either **A** or **a**, never both. If two factors are involved, as in an **AaBb** plant the gametes will be **AB**, or **Ab**, or **aB**, or **ab**, never **Aa**, **Bb**, **ABb**, **Aab**, and so on. All possible combinations will be obtained, consisting of one member of each pair of genes. Every type of gamete will be produced in equal frequency.

It must be remembered that, without further work, these conclusions could apply only to the seven pairs of pea genes actually studied by Mendel. The fact that Mendel's rules applied to these would indicate that other genes of peas *might* behave in a similar way. The discovery that rules of inheritance could be established for peas would suggest that the same or similar rules might also apply to other plants (and possibly animals). This, of course, would have to be tested by experimentation. The great worth of Mendel's theory was that its clear and definite formulation made testing by experimentation possible. The same could not be said for any previous theory of inheritance.

Most of the important discoveries in biology turn out in retrospect to be fairly simple. Inevitably we wonder, Why did not that idea occur to someone before? Why had no one discovered these simple relations when varieties were crossed? Why had no one realized the significance of Mendel's approach during the 34 years between 1866 and 1900? These are unanswerable questions, but the following facts are germane to the last one. Mendel was almost unknown among biologists during his day and his results were published in a journal that attracted little attention. This is clearly only part of the story. It is perhaps more correct to say that biologists in 1866 were unable to appreciate the significance of Mendel's work. Their minds were not prepared. There is one interesting bit of information in this connection. Mendel carried on a lengthy correspondence with Nägeli, explaining the results of his experiments. It should be remembered that Nägeli was greatly interested in heredity, he being the proponent of the idioplasm concept. He, of all people, should have seen Mendel's point but he failed to appreciate the significance of the pea experiments.

Still another fact is that Mendel did not believe for long in the universality of his findings. This was the result of an unfortunate choice of material, the hawkweed, which was recommended to him by Nägeli for some additional experiments. In the hawkweed the ovules are capable of parthenogenetic development. As a result, many of the crosses he believed he was performing were not crosses at all. Mendel did not realize this and was unable to understand why he did not observe the ratios he had previously found in peas. He probably came to believe that his results held for peas alone. Mendel and his ideas were of no importance during the last third of the nineteenth century when students of inheritance concerned themselves mainly with the cycle of chromosomal behavior in meiosis, fertilization, and the mitotic divisions during development.

In the last few years before 1900, the three scientists who were to rediscover Mendel's work were experimenting with crosses of varieties of plants. Two of them, Hugo de Vries (1848–1935) and Carl Correns (1864–1935), independently discovered Mendel's rules of inheritance before they knew of Mendel.

In 1900, de Vries reported the results of hybridizing varieties of 15 species of plants. When one member of the parental generation was dominant and the other recessive, the F_1 generation always resembled the dominant parent. In the F_2 generations, he observed the 3:1 ratio that Mendel had found long before: the number of recessives in the 15 crosses varied from 22 to 28 per cent, averaging 24.93 per cent. De Vries emphasized the critical point that, in the F_1 individuals which have dominant and recessive genes, the gametes are *pure*, that is, they have only one sort of gene, never both. This phenomenon, the Purity of the Gametes, was to be a matter of contention for years. What could the mechanism possibly be? It was difficult to accept any biological phenomenon for which there seemed to be no mechanism.

Carl Correns conducted extensive crosses among varieties of corn and peas and also published in 1900. In most instances he obtained the same results as had Mendel. There were exceptions, however. In a few instances there was no dominance: the F_1 individuals were intermediate in appearance. Correns reported also that Mendel's Law of Segregation did not always apply, though in the majority of cases it did. Since segregation was the usual result, however, he wondered how it might come about. Thus in an F_1 hybrid, which might be symbolized Aa how could the gametes come to contain either A or a , never both? And what could account for the fact that the breeding results indicated that the ratio of A to a is 1:1? He made the tentative and prophetic suggestion that the chromosomes could be responsible. Thus, segregation could be based on the separation of chromosomes at a nuclear division, quite possibly the one in meiosis that Weismann referred to as the reduction division.

Clearly there was more to Mendel's laws than peas.

Confirmations and Exceptions to Mendel's Scheme. In the first few years after 1900, when Mendel's findings became widely known to biologists, the results of many crosses were reported. The majority of these gave ratios that were nearly identical with Mendel's pea crosses. That is, in a cross of a pure-breeding dominant and a pure-breeding recessive, the F_1 population consisted only of plants with the dominant characteristics. The F_2 of such a cross contained both of the original types, in the ratio of three dominants

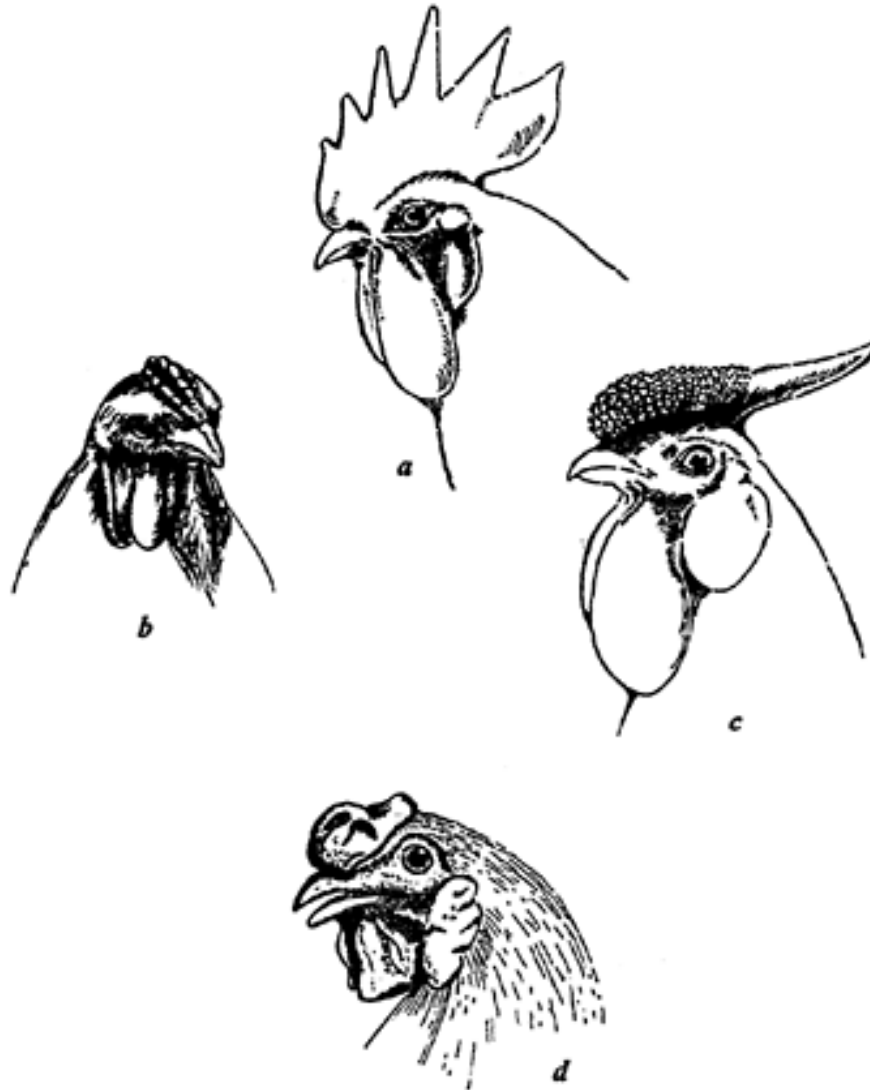
to one recessive. If one of the F_1 plants was crossed with a pure recessive, the ratio of dominants to recessives in the offspring was 1:1. If two pairs of contrasting characters were involved, the F_2 ratio was 9:3:3:1. If the F_1 of the cross just mentioned was crossed to a double recessive, the ratio was 1:1:1:1.

A few gave slightly different results that could be understood with minor adjustments of the Mendelian scheme. Still others defied explanation at that time. This last group of cases was put aside in the hope that eventually a modified Mendelian theory could explain the results. Subsequent events showed this to be a profitable procedure.

In these early years of the twentieth century, the British geneticist, William Bateson (1861–1926), was the most vigorous disciple of Mendelism. Even before Mendel's work was known to the scientific world at large, Bateson had undertaken an extensive program of breeding. As a result of this preparation, he was in a proper frame of mind to grasp the significance of Mendel's work. In England, Bateson waged a scientific battle to convince his fellow biologists that Mendel's approach to the problem of inheritance was a useful one. This 'battle' was not always waged with the fairness, objectivity, lack of bias, and honest criticism that should be the basis for scientific discussions. In fact, the participants behaved like ordinary human beings. Much of the genetic work of this period was summarized in reports Bateson made to the Royal Society (1902, 1905, 1906, 1908, 1909) and in his book, *Mendel's Principles of Heredity* (1909).

Some Useful Genetic Terms. Bateson and others introduced some terms that are useful in describing genetic events. From Mendel's experiments he 'reached the conception of unit-characters existing in antagonistic pairs. Such characters we propose to call *allelomorphs* [now called *alleles*], and the zygote formed by the union of a pair of opposite allelomorphic gametes, we shall call a *heterozygote*. Similarly, the zygote formed by the union of gametes having similar allelomorphs, may be spoken of as a *homozygote*.'

To use these terms in examples, we might observe that in peas *round* and *wrinkled* genes are alleles; so are *yellow* and *green* genes. A pure-



3-1 Combs of fowls. a. *single*. b. *rose*. c. *pea*. d. *walnut*. (From T.H.Morgan. 1919. "The Physical Basis of Inheritance." Lippincott.)

breeding *round* plant, which we have designated **RR**,* is homozygous. A *wrinkled* plant, **rr**, is also homozygous. The F_1 of a cross of these is **Rr** and heterozygous. Recalling that *round* is dominant, we know that a *round* plant can be either homozygous (**RR**) or heterozygous (**Rr**), and that one could not tell by external appearance which was which. It is worth repeating that there is a difference between appearance and genetic make-up. We speak of the appearance of the organism as its *phenotype* (*yellow* or *green*) and the genetic make-up as its *genotype* (**RR**, **Rr**, or **rr**). The individual factors of inheritance, **R** or **r**, carried on the chromosomes are the *genes*.

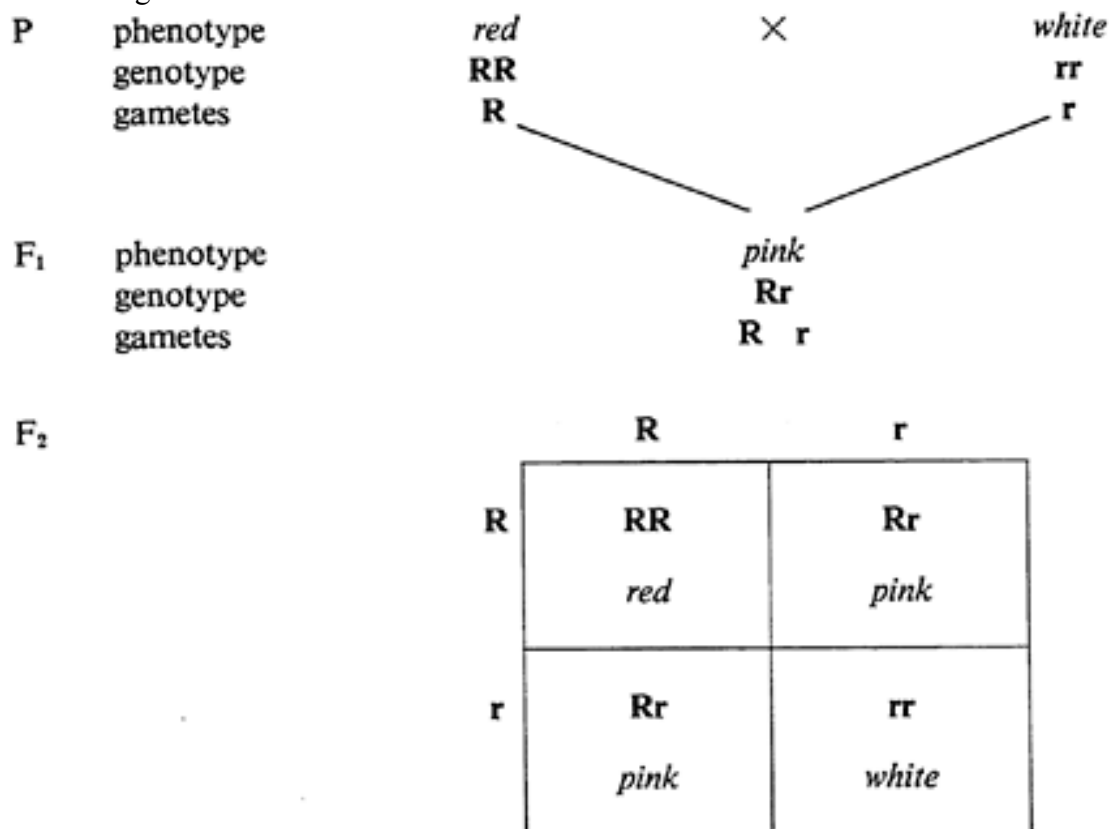
* Heretofore we have been following Mendel's method of notation and used **R**, rather than **RR**. In 1900 both would have meant the same. Other studies, being carried out in the early 1900s, suggested that **RR** is a more accurate way of designating a pure-breeding dominant individual. The reasons will be given in the next chapter.

Returning now to Bateson, these are some of the types of genetic data he gave:

EXCEPTIONS TO THE MENDELIAN RATIOS

1. **Blended Character Expression in Heterozygotes.** In Mendel's results the

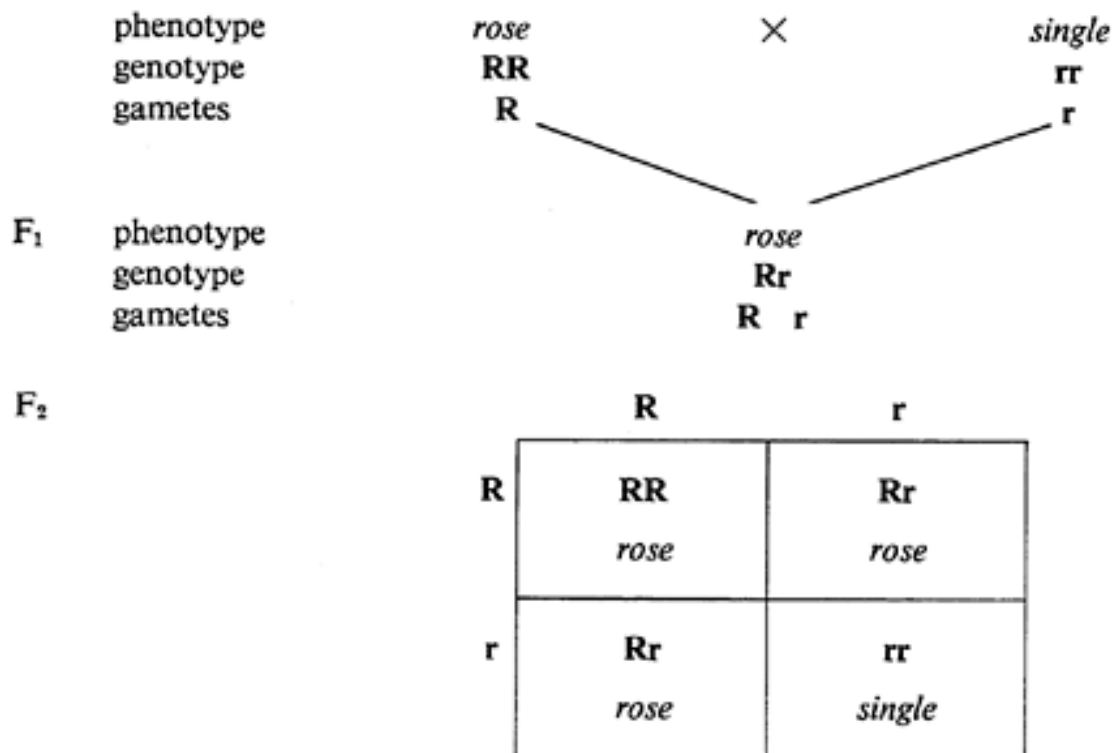
heterozygote was always identical in appearance with the homozygous dominant. Even today we recognize this as the most frequent condition, but there are some cases where the heterozygote is intermediate. In such a situation neither allele is dominant or recessive. One example is a common cultivated flower, the four o'clock. When a *red*-flowered four o'clock is crossed with a *white*-flowered one, all of the F_1 plants have *pink* flowers. In the F_2 , *red*-, *white*-, and *pink*-flowered plants appear. The genetic basis of this cross is diagrammed below:



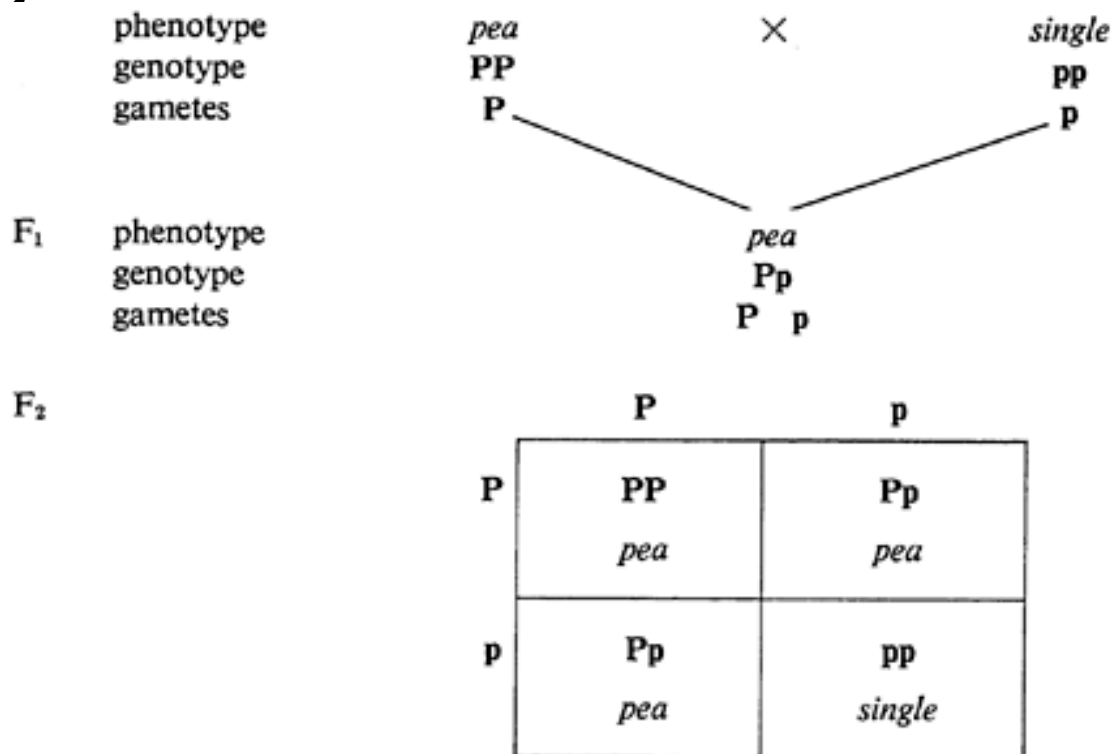
F₂ ratio: 1 *red*, 2 *pink*, 1 *white*.

2. Two Pairs of Alleles Affecting the Same Character. In all the crosses considered so far, a character has been affected by only one pair of alleles. This may seem to imply that every character of an organism is determined by a single pair of alleles. This is not the case, as shown by some experiments with chickens which were reported by Bateson.

Poultry breeders recognized a number of comb types, usually involving differences in comb shape. Some of these types were called *single*, *rose*, *pea*, and *walnut* (Fig. 3-1). A cross between *rose* and *single* gave *rose* in the F_1 and 3 *rose* to 1 *single* in the F_2 . *Rose* and *single* behaved as ordinary alleles with *rose* the dominant.



Similarly, a cross between *pea* and *single* gave *pea* in the F₁ and 3 *pea* to 1 *single* in the F₂. *Pea* and *single* behaved as ordinary alleles with *pea* the dominant.



Considered separately there is nothing unusual about these crosses. Considered together there is one puzzle, largely semantic: why is the genotype of *single* written as **rr** in the first cross and as **pp** in the second? The answer to this question hinges on the fact that the

single comb condition results from the interaction of two different genes. The two previous crosses and the next one to be described show that both the **r** and **p** genes are involved in the genetic determination of comb shape (subsequent experiments showed that additional genes were concerned). A comb of the *single* type forms in a chicken when both the *pea* and *rose* genes are recessive. The genotype of a *single* comb chicken, therefore, is **pprr**. A *pea* comb chicken would have the genotype **PPrr** or **Pprr** and a *rose* comb chicken would have the genotype **ppRR** or **pPrr**. We might have written the cross of *rose* comb × *single* comb as **ppRR** × **pprr**. At that time, however, we were unaware of the existence of the **p** genes. Furthermore, there was no need to do so since both parents are of the same genotype with respect to the **p** gene: by convention geneticists use the symbols only for those cases where the genes differ in the two parents. If the cross involves differences in both the **p** and **r** comb shape genes, then the necessary genetic symbols must be employed. Such a cross will now be described.

Let us cross the two dominants, *rose* and *pea*. The F_1 will be found to have a new type of comb, *walnut*, which might be looked upon as a blending of the two dominant shapes. The F_2 will give a ratio of 9 *walnut*, 3 *rose*, 3 *pea*, and 1 *single*.

The *single* comb is the result of both (recessive) **p** and **r** genes being homozygous. *Rose* is obtained if the animal is homozygous or heterozygous for **R** and homozygous for **p**. *Pea* is obtained if the animal is homozygous or heterozygous for **P** and homozygous for **r**. *Walnut* results when there is at least one **P** gene together with at least one **R** gene.

3. Yellow Mice. Cuénot reported some crosses in mice that neither he nor Bateson could explain in the usual Mendelian manner. He worked with *yellow* and *agouti* hair color genes. These two types of crosses will demonstrate the problem.

1. *yellow* × *yellow* gives 2 *yellow* to 1 *agouti*.

2. *yellow* × *agouti* gives 1 *yellow* to 1 *agouti*.

Cuénot found it impossible to obtain a strain of *yellow* mice that would breed true. The *yellow* animals always behaved as though they were heterozygous. His *agouti* strains bred true. During the course of his experiments he observed that the litter size in crosses of *yellow* × *yellow* was smaller than in the *yellow* × *agouti* cross.

Can you devise a hypothesis to explain the results? From the data given it is possible to arrive at the explanation that was later found to be correct.

4. Coupling of Genes. Bateson listed another discovery that could not be explained, namely, cases involving two pairs of genes that did not show independent assortment. Let us assume that there are two pairs of genes, **A** and **a** and **B** and **b** and that the phenotypic expression of **A** is *A*, that of **a** is *a*, and so on. In the cross **AABB** × **aabb** we should expect an F_2 phenotypic ratio of 9 *AB*, 3 *Ab*, 3 *aB*, and 1 *ab* if Mendel's rules applied. In some crosses, however, Bateson found that the *A* and *B* characters appeared to be completely *coupled*, that is, they were inherited together. The same was true for *a* and *b*. In fact, the F_2 ratios might be close to 3 *AB* to 1 *ab* with few or no individuals of the *Ab* or *aB* phenotypes. Results of this sort could not be accounted for by the Mendelian scheme.

Limitations of Mendelism. A biologist who restricted himself solely to a Mendelian

approach, that is, to a study of the inheritance of 'unit characters' as expressed in the ratios observed in succeeding generations, could make considerable progress. He could study numerous sorts of animals and plants and observe the instances where Mendel's rules held and when they did not. Many individuals restricted their investigations in this way: Bateson and his coworkers were among them. But one soon realizes that the prospects for a deeper understanding of inheritance are limited.

Mendelism really bothered many biologists: it seemed so at variance with the phenomena they usually observed. They knew of few instances that exhibited the extraordinary mathematical exactness that one could easily observe in Mendelian crosses. Furthermore, biologists seek to identify the physical (i.e. structural) basis of phenomena. What in the organism and its gametes could be responsible for Mendelian inheritance? Could it be gemmules or an idioplasm behaving in some exact manner? How could one possibly account for the 'purity of the gametes,' that is, for an **Rr** individual to produce either **R** or **r** gametes but never **Rr** gametes—and to produce them in such exact ratios?

The answers lay elsewhere.

Suggested Readings

Chapter 3 of *Readings* contains long excerpts from the report that Bateson made to the Royal Society in 1902, in which he gave a detailed account of Mendel's experiments and adds much new data. A paper by T.H.Morgan, questioning the basic tenets of Mendelism, is also reproduced.

DUNN, L.C. 1965. *A Short History of Genetics*. New York: McGraw-Hill.

MENDEL, GREGOR. 1866. 'Experiments on plant hybrids.' (See Stern and Sherwood)

OLBY, ROBERT C. 1966. *Origins of Mendelism*. New York: Schocken Books.

STERN, CURT, and EVA R.SHERWOOD. Editors. 1966. *The Origins of Genetics. A Mendel Source Book*. San Francisco: W.H.Freeman. Translations of papers by Mendel, de Vries, and Correns; Mendel's letters to Nägeli; Fisher's attack on Mendel and Wright's reply ; and references to Mendel's experiments in Focke's monograph on plant hybrids.

STURTEVANT, A.H. 1965. *A History of Genetics*. New York: Harper and Row.

Questions

1. Four desirable features for experimentation are listed for Mendel's peas. Why is each desirable?
2. In a plant of the genotype **Rr Yy**, Mendel assumed that the gametes could only be **RY**, **Ry**, **rY**, and **ry**. According to his scheme, **Rr Yy**, **Rr Y**, **Rr**, and **Yy** could not be formed. What is the basis of his belief that such gametes could not be formed? Can you devise a mechanism that would allow some types of gametes to form (i.e. **RY**, **Ry** etc.) but not others (i.e. **Yy**, **Rr**)? (If you already know what the solution eventually proved to be, ignore it, and try to devise other mechanisms.)
3. Account for the fact that pre-Mendelian hybridizers found blending to be a rule of inheritance but that Mendel did not.
4. What do the phenomena of dominance-recessiveness, segregation, and independent assortment tell us about the Mendelian units of inheritance?

5. How do you suppose Aristotle (*Readings, Chapter 1*) would have reacted to Mendel's experiments?
6. A pea plant that is *yellow* and *round* is crossed with one that is *green* and *wrinkled*.
The offspring are:
1/2 *yellow, round*
1/2 *green, round*
What was the genotype of the parents?
7. In another cross of peas the offspring are:
3/8 *yellow, round*
3/8 *yellow, wrinkled*
1/8 *green, round*
1/8 *green, wrinkled*
What was the genotype and the phenotype of the parents?
Hint. When doing genetic problems of this type, it is best to solve for one character at a time. It is necessary, also, to remember how the usual genetic ratios are obtained. Thus, a 3:1 ratio is the consequence of crossing two heterozygotes, **Aa**×**Aa**. A 1:1 ratio is the consequence of crossing a heterozygote and a homozygous recessive, **Aa**×**aa**.
8. In man *brown eyes* (**B**) is dominant over *blue* (**b**). (The genetic situation is not quite this simple but, in doing the following problems, assume that it is.)
 - a. A heterozygous *brown-eyed* woman marries a *blue-eyed* man. What will be the genotypes and phenotypes of the children?
 - b. The first child of two *brown-eyed* parents has *blue* eyes. What are the genotypes of the three individuals? What other genotypes, and in what proportion, might be expected in future children of these parents?
 - c. In a family of nine children two have *blue eyes* and seven have *brown* eyes. What are the probable genotypes and phenotypes of the parents?
9. How might Mendel have accounted for the pattern of inheritance described by Darwin for color blindness (pages 12, 15)? For the porcupine man (page 9)?
10. What evidence can be cited to show that two alleles are not modified by their occurrence together in a heterozygous individual?
11. Can you modify Darwin's Theory of Pangenesis in such a way that it will account for the results obtained by Mendel?
12. Before Mendel's work was rediscovered in 1900, many biologists held the hypothesis that the nucleus was responsible for inheritance. Do Mendel's results support this hypothesis?
13. A *walnut* rooster, heterozygous for both *rose* and *pea*, is crossed with a hen having a *single* comb. What will be the genotypes and phenotypes of the offspring?
14. A *walnut* rooster is crossed with a *rose* hen. The offspring are:
3/4 *walnut*
1/4 *pea*
What were the genotypes of the parents?
15. Did you formulate a reasonable hypothesis to account for inheritance in *yellow* mice?

16. A Mendelian cross of the type **Aa**×**aa** gives a 1:1 ratio. In man, and most other animals, the ratio of females to males is also 1:1. Evaluate this hypothesis: The inheritance of sex is an example of a simple Mendelian cross.

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