Mendelism & Evolution
E. B. Ford
From Macmillan's Monographs on Biological Subjects
THIS book was written a quarter of a century ago to combat a fallacy dangerous at that time but now rejected by all who are qualified to express an opinion. For it was then seriously doubted if Mendelian segregation could provide the type of variation upon which natural selection, as conceived by Darwin, operates. Rather, it was held by many that the mutation of the genes gave substantial support to the various mutational theories of evolution: those of Lamarck and of de Vries among them. Apart from such naive speculations as these, the fruits of faulty deduction and of ignorance, it was widely supposed in the earlier part of this century that Mendelism was irreconcilable with the concept of slow and 'continuous' evolution.

To the splendid achievements of Sir Ronald Fisher, so clearly demonstrating the contrary, was added this modest book, its title *Mendelism and Evolution* proclaiming its aim. 'Genetics and Evolution' would be the correct form today, but it would have been less appropriate then.

It is, of course, obvious that many genetic phenomena, such as polyploidy and polymorphism, fundamental to the mechanism of evolution, are non-Mendelian in the sense that they were not envisaged in Mendel's laws. They are, however, wholly consistent with particulate inheritance and the low mutation rates which this requires, which the mutational theories of evolution are not.
It is hoped that this book can still serve as an introduction to some aspects of evolutionary genetics, even though Mendelism is no longer held to be inconsistent with natural selection in the Darwinian sense. The continued demand for it seems to justify that view, and Messrs. Methuen and Company have kindly allowed me to rewrite the last chapter, and to adjust correspondingly the Bibliography and Index now that a Sixth Edition is required. This has already been done once (for the Third Edition), while the rest of the work remains almost untouched as it first appeared. For that there is a sound reason. The earlier chapters develop principles which, being fundamental, are still essential. The final one consists of deductions based upon them, the interest of which naturally shifts with the advance of knowledge. I have now focused it upon the study of wild populations in which large selective forces are operating: a subject to which much attention has been given by my colleagues, Dr. Kettlewell, Mr. McWhirter and Dr. Sheppard, and by myself. We believe that a combination of ecological and genetic methods when applied to instances of this kind will provide one of the most powerful tools for the analysis of organic evolution.

E. B. F.

OXFORD
May, 1956

PREFACE TO THE EIGHTH EDITION

THIS book has been extensively revised in the eighth edition so as to bring it into line with modern advances in evolutionary genetics.

E. B. F.

Oxford
December, 1964
# CONTENTS

<table>
<thead>
<tr>
<th>Chap.</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preface</td>
<td>vii</td>
</tr>
</tbody>
</table>

## PART I. INTRODUCTION

I The Particulate Theory of Inheritance  
1. The Laws of Mendel  
2. The Physical Basis of Inheritance  
   A. Segregation  
   B. Independent Assortment  
   C. Linkage  
   D. Sex-Linkage  
   E. Crossing-over  
   F. Mutation  
   G. Cistrons  
   H. Supra-genes

## PART II. MENDELISM AND EVOLUTION

II Heredity and the Environment  
1. The External Environment  
2. The Internal Environment  
3. Summary

III Experimental Genetics and Its Bearing on Evolution  
1. The Phenotypic Effects of Mutation
MENDELM AND EVOLUTION

PART I

INTRODUCTION

CHAPTER I

THE PARTICULATE THEORY OF INHERITANCE

1. THE LAWS OF MENDEL

THE Particulate Theory of Inheritance is due to the genius of Gregor Mendel, a member, and subsequently Priest, of the Konigskloster at Brunn (now Brno) in Moravia. He communicated the results of his work on heredity to the Brunn Natural History Society in 1865, and they were published in its Transactions the following year. It is remarkable that this now famous paper passed unnoticed at the time, for it did not attract attention until 1900, sixteen years after its author's death.

Mendel left his conclusions in the form of two very simple laws. First, that when pure-bred individuals exhibiting a pair of contrasted characters are crossed, the original types separate out in definite proportions in the second filial generation, that is among the grandchildren. This process he called Segregation. It makes no difference what may happen in the first generation of the cross. This is made up of hybrid individuals; one of the two characters may be obscured by the
other, or some condition intermediate between them may be found. The essential is that no blending has occurred, as is proved by the recovery of the grandparental types in half of the next generation, the remainder being again of the hybrid constitution.

Secondly, Mendel asserted that when two or more pairs of contrasted characters are brought into the cross they segregate independently of each other. This principle, known as the law of Independent Assortment, has, however, been somewhat modified by subsequent discoveries, as will be described in the section on Linkage.

In Mendel's day the phenomenon of segregation, and the constant numerical ratios in which the different types crystallize out of the hybrid mixture, could not be correlated with any known mechanism. But in the thirty-five years which elapsed before his results attracted general attention, great advances had been made in cytology. It had become apparent that the hereditary material must be carried in the nucleus of the germ cells, for this is often the only part which the offspring receives from both its parents. And in the nucleus had been found self-perpetuating bodies, the chromosomes, which exist in pairs, whose members, having separated from each other, are recombined at fertilization in a manner well fitted to provide the physical basis of the Mendelian segregation of characters.

This close parallel between the genetic requirements and the facts of cytology was first pointed out by Sutton (1902). Later work, especially that of the Morgan school, has built up a vast body of facts which make the evidence for the chromosome basis of heredity remarkably complete. It may therefore be of value to give a short account of Mendel's two laws in the light of these discoveries.
2. THE PHYSICAL BASIS OF INHERITANCE

A. Segregation. Inherited characters are dependent on the action of certain genetic factors or 'genes' which control them. These are present in pairs, whose members are derived one from the father and the other from the mother of each bi-sexually produced individual. The paired genes are carried in paired bodies, the chromosomes, of which every somatic cell in the organism has a complete set in its nucleus. The mature germ cells, however, contain but one member of each chromosome-pair, consequent upon 'meiosis', a process in which the partners conjugate, separate, and pass at random to opposite poles during cell-division, there to be carried into different cells by the constricting cytoplasm. The total number of chromosomes, and therefore of genes, is restored when the gametes, each possessing half, fuse at fertilization.

The members of each factor-pair are called 'allelomorphs', and from what has already been said, it is evident that they are carried in different but homologous chromosomes; that is, in chromosomes which form one of the conjugating pairs. At rare intervals the chemical or physical nature of a gene may change. This process, known as 'gene mutation', is indeed responsible for the fact that the members of allelomorphic pairs may exist in two or more conditions, giving rise to contrasted variations in the characters which they produce. A number of such changes may sometimes occur in the same gene and so form a series of 'multiple allelomorphs'. Only two of the members of such a series can, of course, normally be present at the same time.

If the members of an allelomorphic pair are of similar nature they are said to be 'homozygous', if dissimilar 'heterozygous'. In the latter event their effect may
MENDELISM AND EVOLUTION

be intermediate between that which either produces in
the pure, or homozygous, condition or, more generally,
the presence of one type may obscure the action of
the other. The former is then known as a 'dominant'
and the latter as a 'recessive' character.

It is evident, however, that whatever the hetero-
zygous effect may be, no blending has occurred. For
owing to meiosis during maturation, the unlike members
of the factor-pair segregate from each other in the
separating chromosomes, to produce germ cells carrying
either one or the other type, thus giving rise to fresh
combinations in the next generation.

An example will make this clear. In natural condi-
tions the eyes of the Amphipod Gammarus chevreuxi are
made up of black facets separated from each other by
white pigment. A mutation has however occurred, the
effect of which is to make the facets red instead of
black; when animals of this type are mated together
they always breed true. If a pure-bred black-eyed
Gammarus is mated with a red-eyed individual, all the
resulting family, which constitute the first filial (F1)
generation, have black eyes. Therefore the black-eyed
condition found in nature is dominant to the red-eyed,
which arose by mutation in the laboratory. When these
F1 animals are interbred, segregation occurs among
their offspring, the second filial (F2) generation, accord-
ing to the first law of Mendel, for three-quarters of
them have black and one quarter red eyes.

The recessive character has thus been recovered from
the hybrid condition, and such 'extracted recessives' when
mated with similar individuals are permanently
true breeding like their red-eyed grandparent of the
F1, or first-parental, generation. The other grand-
parental type, which breeds true for the black-eyed
character, is also recovered, and in the same proportion,
for it is also found in one quarter of the F2 generation. The remainder, half in all, are heterozygotes similar to the F1 individuals. Consequently they do not breed true but, as before, when interbred one quarter of their offspring have red eyes.

This result is at once intelligible on the chromosome hypothesis. The true breeding black-eyed and red-eyed conditions are each dependent on a pair of allelomorphic factors homozygous for the genes concerned. If the factor for black eyes be represented by \( R \) and that for red eyes by \( r \), then each cell of the pure black-eyed animal must contain the factors \( RR \), and of the red-eyed \( rr \). These pairs, being allelomorphic, are situated in homologous chromosomes, and they separate from each other during meiosis when the chromosome number is halved. In consequence, the germ cells of the pure black- and red-eyed types contain only one member of each factor-pair; that is, \( R \) and \( r \) respectively.

When a black-eyed and a red-eyed \textit{Gammarus} are mated, the original number of chromosomes, which has been halved in the germ cells, is of course restored at fertilization. The character with which we are concerned, facet colour, is now once more represented by a pair of factors. But this is a heterozygous pair of the constitution \( Rr \), made up of \( R \) from one parent and \( r \) from the other. At meiosis, therefore, when the allelomorphs separate again, the germ cells of this, the F1, generation receive either the factors \( R \) or \( r \). The chances therefore are equal that either type of ovum may be fertilized by either type of spermatozoon. That is to say, a spermatozoon carrying \( R \) may meet an ovum carrying \( R \) or \( r \), so giving either the combination \( RR \) or \( Rr \); so also may one of the equally numerous \( r \)-bearing spermatozoa, giving either the combination
Three classes of zygotes, then, are possible, \( RR, Rr, \) and \( rr \), in the proportion 1:2:1.

One quarter of the F2 generation are therefore extracted recessives (\( rr \)) with red eyes, one quarter extracted dominants (\( RR \)) with black eyes, and one half heterozygotes (\( Rr \)). These also have black eyes, since, in this instance, dominance is complete. They are indistinguishable from the homozygous black-eyed class but do not breed true. Black- and red-eyed animals thus appear in a ratio of 3:1 in the F2 generation.

This result was obtained by producing heterozygotes and mating them with each other. But it is evident that segregation will also occur if heterozygotes are mated with either of the homozygous types. Such a mating is known as a "back cross", for it is produced when the F1 (heterozygous) generation is crossed back to one of the parents, or indeed to any other homozygous individual; the offspring so obtained are said to constitute the F2 generation.

This may be illustrated from the example already discussed. The heterozygous black-eyed Gammarus carry the factor-pair \( Rr \) and, after maturation, half their germ cells possess the \( R \) and half the \( r \) factor. The homozygous red-eyed type is of the constitution \( rr \) and must produce germ cells all carrying the \( r \) factor. Therefore, on mating, the chances are equal that a germ cell of the latter kind, necessarily carrying the \( r \) factor, meets one of the former with either the \( R \) or the \( r \) factor. Consequently half the offspring have the constitution \( Rr \) and half \( rr \); half are black and half red-eyed.

Thus segregation occurs in the generation produced by a back cross, the two contrasted characters appearing in equal numbers. It is seen, then, that a ratio of 1:1 is characteristic of the F2 generation, just as a ratio of either 1:2:1 or 3:1, depending on whether domin-
The facts so far described can now be summarized in two diagrams (Figs. 1 and 2).

B. Independent Assortment. In his second law Mendel stated that two contrasted characters behave independently of each other when inherited together. From what has so far been said of the mechanism of heredity the truth of this statement must be obvious, so long as the factor-pairs in question are situated in different pairs of chromosomes. In such circumstances their allelomorphs will segregate from each other during meiosis and pass into the germ cells at random.

It is evident that when individuals with two contrasted pairs of characters, each exhibiting complete dominance, are crossed, four types will be produced in the F2 generation. These represent the original distribution of the characters and the two possible recombinations between them. Since each type, considered separately, will appear in a 3:1 ratio in this generation, the four will together be present in a combination of two such ratios; that is to say in a ratio of 9:3:3:1.

To make this plain, we will consider the example of the pair already studied, black (dominant) compared with red facets in the eyes of *Gammarus chevreuxi*, and combine it with another pair of factors of quite similar inheritance carried in different chromosomes. Such are the factors controlling the appearance of white pigment surrounding the facets; the presence of this pigment, the normal condition, being dominant, and its absence recessive.

If a *Gammarus* pure-bred for the black-with-white characters be mated with one having red facets and no surrounding white pigment, the offspring will receive one member of each of the chromosome pairs carrying
MENDELM AND EVOLUTION

FIG. 1.—Segregation in the second hybrid generation (F2) of a cross between two contrasted characters; black (dominant) and red (recessive) colour in the eyes of the Amphipod Gammarus chevreuxi.

![Diagram of Mendelian segregation in F1 and F2 generations.]

FIG. 2.—A back-cross (heterozygote × homozygote), showing segregation in a 1:1 ratio in the resulting (R2) generation. The characters are the same as those in Fig. 1.
these factors, and will be double heterozygotes in constitution. In appearance their eyes will be black with white pigment, for the two dominant characters will, of course, express their effect. Consequent upon the meiosis of this, the F1 generation, each gamete will receive haphazard one member of each chromosome-pair. Four types of gametes are thus formed in equal numbers. For the chances are equal that the factor for the production of the black facets is included with that for the presence or for the absence of the white pigment, so also for the equally numerous factors for the production of red facets.

The chances also are equal that at fertilization any of these four types of gametes formed by one sex meet any of the four formed by the other; sixteen types of zygotes are thus produced in equal numbers. Of these nine will contain one member at least of each dominant pair, three will be without one dominant type and three without the other, while one will have all its factors recessive.

In order to make these facts quite clear they can now be expressed in two diagrams, Figs. 3 and 4. \( R \) and \( r \) will again be used for the factors producing black and red facets respectively, while that producing white pigment outside the facets can be represented by \( W \) and its recessive allelomorph by \( w \). The members of each factor-pair thus have the same symbols, the capital letter being used for the dominant.

Besides illustrating the facts already described, Fig. 4 demonstrates several other points. It is, for example, to be noticed that only one quarter of the F2 generation would be true breeding if mated to individuals similar to themselves, but this comprises one member of each of the visibly distinct types. Further, individuals homozygous for both dominant and both recessive
factors respectively occur only in one-sixteenth of this generation. The important result obtained by making a back-cross involving two pairs of independently assorting factors will also be apparent. Fig. 3 illustrates that a double heterozygote produces four types of germ cells in equal numbers, and it is evident that when both pairs of factors are homozygous only one type of germ cell can arise. A cross between a double heterozygote and a double recessive therefore produces an R2 generation in which the four visibly distinct forms appear in equal numbers.
In the present instance the germ cells formed by the double recessive (rrww) will all be of the constitution

<table>
<thead>
<tr>
<th>F1 germ cells</th>
<th>RW</th>
<th>Rw</th>
<th>rW</th>
<th>rw</th>
</tr>
</thead>
<tbody>
<tr>
<td>RW</td>
<td>RRWW</td>
<td>RRWw</td>
<td>RRWW</td>
<td>RrWw</td>
</tr>
<tr>
<td></td>
<td>black</td>
<td>black</td>
<td>black</td>
<td>black</td>
</tr>
<tr>
<td></td>
<td>with white</td>
<td>with white</td>
<td>with white</td>
<td>with white</td>
</tr>
<tr>
<td>Rw</td>
<td>RRWw</td>
<td>RRWw</td>
<td>RRWw</td>
<td>Rrw</td>
</tr>
<tr>
<td></td>
<td>black</td>
<td>black</td>
<td>black</td>
<td>red</td>
</tr>
<tr>
<td></td>
<td>with white</td>
<td>with white</td>
<td>with white</td>
<td>with white</td>
</tr>
<tr>
<td>rW</td>
<td>RrWw</td>
<td>Rrw</td>
<td>rrWw</td>
<td>rrww</td>
</tr>
<tr>
<td></td>
<td>black</td>
<td>red</td>
<td>red</td>
<td>red</td>
</tr>
<tr>
<td></td>
<td>with white</td>
<td>with white</td>
<td>with white</td>
<td>with white</td>
</tr>
<tr>
<td>rw</td>
<td>Rrww</td>
<td>rrww</td>
<td>rrww</td>
<td>rrww</td>
</tr>
<tr>
<td></td>
<td>black</td>
<td>red</td>
<td>red</td>
<td>red</td>
</tr>
<tr>
<td></td>
<td>with white</td>
<td>with white</td>
<td>with white</td>
<td>with white</td>
</tr>
</tbody>
</table>

*F1 generation = 9 black with white, 3 black no white, 3 red with white, 1 red no white.*

**Fig. 4.—Recombination at fertilization of the F1 germ cells, whose formation is illustrated in Fig. 3. They produce an F2 generation in which four types appear, segregating in a 9:3:3:1 ratio.**

*rrww. The combinations between these and the four types produced by the double heterozygote are illustrated in the lowest horizontal line of Fig. 4.*
C. Linkage. The number of genetic factors in any individual must be very great, amounting at least to several thousand. It is, however, rare to find a species having more than three or four dozen chromosomes, and often there are much fewer. In *Drosophila melanogaster*, the fruit-fly in which so many genetic problems have been studied, there are four, in *Gammarus chironomus* thirteen, and in man twenty-three pairs. It is evident, therefore, that each chromosome must contain many factors. These will be inherited together for, at meiosis, they will pass into the same germ cell without the opportunity of random assortment. This is known as 'linkage'.

If a back-cross is made between two linked factors it is therefore to be expected that only two types will be represented in the R2 generation. The recombination classes will be absent, for free assortment only occurs when the pairs of factors are in different pairs of chromosomes.

It is important to notice that in linkage no association exists between the factors as such, except that they happen to be carried in the same vehicle. Thus two linked homozygous dominants may be brought into a cross by one parent and their recessive allelomorphs by the other. Then, when the F1 generation is back-crossed, the two grand-parental types will appear in R2, in this instance the double dominants and double recessives. If, however, each parent brings in the dominant allelomorphs of one pair and the recessives of the other, on back-crossing to the double heterozygote it is again the grand-parental types which appear; the double dominant and double recessive classes are now absent. The factors which go into the cross together come out together whichever way they may happen to be assorted.
In order to illustrate linkage an example may be drawn from the work on Drosophila melanogaster. The factors for black body-colour (b) and curved wings (c) are carried in the same chromosomes; they are recessive to the normal conditions of grey body (B) and straight wings (C) respectively.

If a pure-bred grey straight-winged fly is mated with one having a black body and curved wings, a double heterozygous F1 generation of grey straight-winged flies is obtained, of which the males produce two types of germ cells only. When mated with double recessive females, to give a back-cross, the two original types appear in equal numbers, and the recombinations between them are not found. This is illustrated in Fig. 5.
Linkage, of course, holds good for all the factors situated in the same pair of chromosomes, however many there may be. Such factors, therefore, are associated together in a 'linkage group'. On the chromosome theory of heredity there can be no more linkage groups in a particular species than there are pairs of chromosomes. Experimental evidence has confirmed this.

D. Sex-Linkage. Sex is inherited as a pair of contrasted characters segregating in a definite proportion which is generally near equality. It therefore partakes of the nature of particulate inheritance and is, in fact, dependent upon the action of one or more genes carried in a particular pair of chromosomes called X-chromosomes. The remaining chromosomes, not directly concerned with the determination of sex, are together known as the autosomes.

In one sex there is a pair of X-chromosomes, just as there is a pair of each of the autosomes. In the other sex there is but a single X-chromosome whose partner is almost destitute of genetic factors and is, in general, not concerned with sex determination, this is the Y-chromosome. Sex, then, is dependent upon a quantitative reaction: two doses of the sex factors carried by the X-chromosomes evoking the development of one of the sexes, while a single dose evokes the development of the other. The former, having similar sex-chromosomes, is known as the homogametic and the latter as the heterogametic sex. It is a highly remarkable fact that the heterogametic sex is in some forms the male, and in others, lepidoptera, the birds, some fishes and amphibians, it is the female.

From what has already been said on the subject of linkage it is to be expected that the X-chromosomes will contain many factors other than those for sex, with which, however, they will necessarily be linked. Such
sex-linked factors, then, are inherited relative to sex, unlike those situated in the autosomes.

Fig. 6 shows the inheritance of a sex-linked factor, white-eye colour (w) in Drosophila melanogaster. It is recessive to the normal red-eyed condition (W). When a white-eyed male is mated to a pure-bred red-eyed female, all the offspring have red eyes; the daughters, however, carry the white-eye factor while the sons do not, for they receive their only X-chromosome from their mother. On interbreeding the F1 generation it is found that red and white eyes appear in a typical 3 : 1 ratio in the F2 flies, but they are not distributed at
random between the sexes as the characters previously considered have been. Half the males, but none of the females, have white eyes like the male grandparent. The appearance of the white-eye character is thus linked with the male sex though inherited through the female. It should be noticed, however, that the appearance of recessive sex-linked characters is not confined to one sex. They appear more frequently in the heterogametic than in the homogametic sex, because in general their effect cannot be swamped by a dominant partner in the Y-chromosome. In the present instance white-eyed females could easily be produced, by mating females heterozygous for this character to white-eyed males.

Fig. 6 also demonstrates the important fact, previously noticed, that sex is determined by a quantitative reaction depending merely on the number of X-chromosomes present. For it is seen that the single X-chromosome of the male is derived from his mother, where it was concerned in producing the female condition. That the Y-chromosome does not determine sex in Drosophila is demonstrated by exceptional instances in which it is lost; this does not affect the development of the male.

E. Crossing-over. Linkage, however, is not always complete, for an exchange of substance, and therefore of genes, may occur between the chromatids derived from homologous chromosomes during the prophase of the first meiotic division. This is known as Crossing-over. At this time the chromosomes become spun out into thin threads (the leptotene stage) which twist round each other. Subsequently each splits longitudinally, forming a pair of 'chromatids'. The evidence indicates that pairs of chromatids, whose members are derived from homologous chromosomes, exchange
The frequency with which this may occur varies with the environment (temperature affects the process) and with the constitution of the individual. In Drosophila, for example, certain genes prevent a breakage occurring in their immediate neighbourhood, while no crossing-over is possible in the males of this genus; indeed in all forms it appears to be less frequent in the heterogametic than in the homogametic sex. On the other hand, the frequency with which a breakage and interchange may occur between any two factors is constant in the same conditions. It is important very briefly to study crossing-over, and the light which it throws on the mechanism of heredity.

If two individuals, one homozygous for the dominant and the other for the recessive allomorphs of two pairs of factors, are mated, double heterozygous offspring are produced. It has been pointed out that when these are back-crossed to the double recessive class, then, if the two pairs of factors are in different pairs of chromosomes, free assortment takes place. The two grandparental types and the two possible recombinations between them all appear in equal numbers.

If, however, the factors are in the same pair of chromosomes, and complete linkage exists, the two grandparental types only will segregate out. But when crossing-over occurs there appear in addition some individuals belonging to the recombination, or cross-over, classes. In order to estimate the amount of crossing-over, these are added together and expressed as a percentage of the whole. This is known as the 'cross-over value'.

When the cross-over values of three factors A, B, C in the same chromosome are studied, it is found that an important relationship exists between them. For the cross-over value between A and C equals either the...
sum or the difference of that between AB and BC. This indicates a linear relation between the three factors in question and allows their order on the chromosome to be determined. It is ABC if $AC = \text{the sum of } AB \text{ and } BC$, while it is ACB if $AC = \text{the difference between them.}$

The closer together any two factors happen to be, the smaller is the chance that crossing-over will take place between them. Thus it comes about that the percentage of crossing-over is a measure of the relative distance of the factors from each other. It has therefore been possible to construct maps showing the order and position of the factors on the chromosomes. Allelomorphic factors are those which lie exactly opposite each other. Thus we arrive at a definition of allelomorphism: allelomorphic factors are situated at identical loci in homologous chromosomes.

It has been established that crossing-over does not take place at single loci but between blocks of factors. Out of the four homologous chromatids, two cross over at any point. An X-like figure, known as a 'chiasma', arises here, due to the interchange between them. It is evident that when two widely separated factors are studied, there is opportunity for crossing-over to occur twice between them, so upsetting the expected crossover value. If, however, the factors studied are close together, the chances of double crossing-over taking place are small. This possibility is even further decreased by the fact that crossing-over at any locus protects the region for some distance on either side of it from coincident crossing-over; as would again be anticipated, for intertwining threads have a modal length of twist. For short distances and small crossover values, therefore, the linear relationship previously indicated between three factors is maintained.

Proofs of the way in which crossing-over occurs and
of the linear order of the genes have been obtained by various methods. A consideration of them is, however, quite outside the scope of this book. Suffice it to say that it has been shown by Plough (1917) that crossing-over actually takes place at the only time when the chromosomes, which may normally be rounded bodies, are spun out into threads and twist round each other. Other work on crossing-over, for example that of Stern (1931), has correlated genetics with cytology in a convincing manner. It is no longer possible to maintain, as has been done in the past (Russell, 1930), that the factors may be due to the action of the individual chromosomes as a whole. For it has been shown that when a piece of one of the chromosomes breaks away, the action of the factors in the remaining portion is normally unaffected; while should the missing fragment become attached elsewhere, it carries its own factors with it and they are uninfluenced by their separation from the major part of their chromosome. Another result of this work has been to enable chromosome maps to be made on cytological evidence (Dobzhansky, 1930a). They confirm those based on genetic evidence.

Finally, in order to make the subject of crossing-over quite clear, an example may be given. In Drosophila melanogaster the factors for pink eyes and curled wings are recessive to the normal conditions of red eyes and straight wings. If a pure-bred fly with red eyes and straight wings be mated to one with pink eyes and curled wings, all the offspring (F1) will have red eyes and straight wings like their normal parent. When females from such offspring are mated to male flies with pink eyes and curled wings, an R2 generation is obtained consisting of 49 per cent. of flies with red eyes and straight wings, 49 per cent. with pink eyes and curled
wings, 1 per cent. with red eyes and curled wings, and 1 per cent. with pink eyes and straight wings. These last two represent the recombination, or cross-over, classes. Added together it is seen that the cross-over value between the pink and curled factors is 2 per cent. Thus they are situated in the same chromosome and at a distance of two units from each other. Had they been in different chromosomes the four classes would have appeared in equal numbers. If, on the other hand, they had been completely linked, as they would have been had the F1 males been mated to double recessive females, only the two grand-parental types would have appeared.

It is to be noticed that in this instance both dominant factors came in from one grandparent and both recessives from the other. At segregation this association was preserved, with rare recombinations. The two dominants and the two recessives thus appear to be coupled together, and such an association is known as Coupling. Repulsion, on the other hand, is said to occur when the two dominants come in from different grandparents; this arrangement tends to be preserved at segregation, and the two dominants and the two recessives appear to be repelled from each other. Coupling and repulsion, though at one time regarded as distinct processes, are therefore seen merely to be manifestations of the same phenomenon.

If individuals doubly heterozygous for two linked factors are interbred to produce an F2 generation, instead of being back-crossed, coupling will give rise to an excess of the first and last classes of what with free assortment would be a 9:3:3:1 ratio. Repulsion would lead to an excess of the two middle terms. Cross-over values of 50 per cent. cannot be distinguished from free assortment. Factors giving this value
would be placed in different linkage groups until one situated between them, to which both would of course be linked, chanced to be discovered. For this reason it has sometimes been reported that a species has more sets of linked factors than pairs of chromosomes. This has never been substantiated, for the true condition has always been revealed by a more detailed analysis.

F. Mutation. Many meanings have been applied to the term mutation. It is, however, convenient to restrict it to the inception of a heritable variation. This may take the form either of a gene mutation, which is a change in a genetic factor, or of a chromosome abnormality.

Gene mutations, then, are responsible for the fact that allelomorphic factors may exist in two or more conditions; they are consequently of fundamental importance in heredity and evolution. They are of very rare occurrence, so much so that it is most difficult to estimate their frequency. Even in Drosophila melanogaster, of which far greater numbers have been studied than of any other animal, such an estimate is rather untrustworthy, for the number detected will greatly depend upon the skill of the observer. It would seem, however, that a given gene seldom mutates in more than one individual in three hundred thousand: usually more rarely. They appear to be completely localized changes. Mutation at one point in a chromosome is not accompanied by simultaneous mutation at other loci nor even in the allelomorphic factor. It can occur in the body cells, as well as in the germ tract, so giving rise to 'somatic mutation'. This results in a mosaic appearance similar to that sometimes produced in heterozygotes by the dropping out of a chromosome, due to a failure in mitosis. When
this occurs in a homozygote it must be attributed to somatic mutation.

Gene mutations can, however, be induced by short-wave radiation from X-rays or radium, and their frequency may be increased at least fifteen or twenty thousand per cent by this means. The rate of increase appears to be proportional to the energy of the dosage absorbed, and is independent of the wave-length (Oliver, 1930). Although the great rarity of mutation in natural conditions throws much doubt on most conclusions based upon its relative frequency, it would seem to be established that some loci are more mutable than others. The greater frequency of gene mutations at the white-eye locus of Drosophila melanogaster, as compared with other loci where only a single change has been detected, is certainly statistically significant. Thus there would appear to be a characteristic mutation rate for each locus. On the whole it seems that those loci which mutate most frequently in normal laboratory conditions produce the most mutations when treated with X-rays. It is possible to suppose, therefore, that the artificial induction of mutation is concerned in raising the general level of the mutation rate.

The causes which bring about mutations in normal conditions are at present quite unknown. It can only be stated that the amount of radiation occurring naturally seems insufficient to account for them (Muller and Mott-Smith, 1930). The important question of the nature and frequency of mutations in laboratory conditions as compared with those in the open will be discussed in Chapter III.

The type of change which occurs at gene mutation has been a subject of much controversy. In the past many workers have been led to the conclusion that a
physical loss of material takes place. That gene mutations, however, must often represent chemical changes rather than physical losses is indicated by the proved fact of reverse mutation. It is hard to conceive of mutations occurring in both directions with a frequency at all comparable to each other if an actual loss were involved in the original change. It has, however, been pointed out (Ford, 1930, pp. 561-2) that some gene mutations may in fact represent physical losses of material. But these are probably exceptional, and the evidence for their occurrence is quite other than that which led to generalizations on this subject in the past.

Chromosome abnormalities may also lead to hereditary changes. These are to be divided into two distinct classes: exceptional fragmentation of the chromosomes themselves, and abnormalities in the distribution of whole chromosomes.

The first of these types occurs naturally, though very rarely. It is, however, quite a frequent result of treatment with X-rays. Portions of chromosomes may break away and become attached either to the homologous chromosome (duplication) or to one of the other chromosomes (translocation), while sections of a chromosome may be lost, so giving rise to deletion. Failures in cell-division, on the other hand, lead to polyploidy, in which more than two members of the chromosomes-pairs are present; or to heteroploids in which either an extra chromosome may be added to the group or one lost from it. A study of the chromosomes in allied species indicates that such irregularities have occurred in nature. It is clear that in certain instances they have been important in evolution (pp. 92-3).

The effect of heteroploidy is generally deleterious since
the genic balance is upset, but a simple multiplication of the chromosome number is free from this defect. The forms in which this has occurred are known as autopolyploids. These are usually fertile with one another, but not with individuals whose chromosome number is a different multiple from their own. Thus they are capable of originating a new stock which may evolve along its own lines and lead to a specific difference.

The chromosomes of a polyploid may, however, be derived from two different species (allopolyploidy). Hybrids between different species should contain the haploid number of each. They are generally sterile, since the chromosomes have no identical partners with which to conjugate during meiosis. If, however, they double this number, producing an allotetraploid, each chromosome gains a partner and fertility is restored. In this way fertile hybrids, sterile with both their parental forms, may be produced. This is a near approach to the formation of a new species. It has occurred under experimental conditions (e.g. in Primula Kewensis, the hybrid between P. floribunda and P. verticillata), and it has done so in nature (pp. 92-3).

Polyploidy, then, has played a part in the evolution at least of plants. But the changes it initiates are often considerable, and then they must generally be disadvantageous (see p. 46). It must be very unimportant in animals, for they are rarely self-fertile and, furthermore, their mobility and quantitative sex-determining mechanism will tend to prevent the establishment of this type of mutation.

G. Cistrons. Since this book was first published it has been discovered that each gene consists of many distinct genetic units, possibly up to 300, at which mutation can take place. Though in linear order, it must not be supposed that these represent an arbitrary group of
those arranged along a chromosome. On the contrary, it is generally true that, instead of being dissimilar in their action, the genetic units within a gene, which are said to constitute a 'cistron', each control the same set of characters; thus they are 'non-complementary' in their action instead of determining distinct qualities in the same individual, as with the action of the various genes. Consequently any intra-cistronic mutation gives rise to identical changes or to multiple alleles. It seems indeed that the cistrons may have been evolved at a remote period, possibly by duplication, to control the development of a given set of characters. The ordinary concept of the genes as the fundamental genetic entities, employed in this book, is indeed still adequate for all purposes except when the evolution and minute structure of the genetic material is under consideration.

H. Super-Genes. It will be evident that, from the evolutionary point of view, heredity must be capable of providing great heritable variability, upon which selection can work, and great heritable stability, so as to preserve advantageous qualities. These two apparently opposed requirements are jointly provided only by the Mendelian system. Yet when that mechanism is described in elementary textbooks, one of these basic aspects is almost always omitted; for it is treated solely as a means for supplying genetic diversity.

Evidently complex evolutionary adjustments, often maintained in alternative phases (see polymorphism, pp. 94–106), necessitate the combined action of several 'co-adapted' major genes. But how are these held together if they assort independently when on different chromosomes and are separated by crossing over when on the same one? That difficulty is resolved by the formation of 'super-genes', one of the fundamental aspects of particulate heredity.
When the co-operation of two or more major genes is required, selection will favour any occurrence which brings them into the same linkage group, by an interchange of segments between non-homologous chromosomes or even by a translocation. It will then favour a reduction in crossing-over between the units concerned. This can be achieved in several ways: by including them within an inversion, which prevents either the formation of cross-over chromatids or their survival, by simply reducing chiasma-frequency between them or else by moving them nearer together by means of chromosome reconstructions. As the linkage between co-adapted genes increases so the selection-pressure required to hold them together diminishes, or holds them the more effectively.

When the amount of interchange between such loci is so reduced that they act effectively as a single unit in segregation, they form a 'super-gene' in which the desired genetic stability is achieved: this, of course, follows at another level, as it were, from the stability of the genes themselves; for these do not contaminate one another when brought together and seldom change intrinsically by mutation.

It seems, then, that a distinction can be drawn between the origin of cistrons, which are non-complementatory in their action, probably ancient and perhaps the result of duplication, and that of super-genes. For these are brought together from different parts of the chromosomes relatively recently to meet the needs of micro-evolution. In view therefore of their action and of segregation, Mendelism meets the paradoxical requirement of supplying at need great heritable variability and great heritable stability.
PART II
MENDELIISM AND EVOLUTION

CHAPTER II
HEREDITY AND THE ENVIRONMENT

1. THE EXTERNAL ENVIRONMENT

The mechanism of heredity has been briefly outlined in the preceding chapter. For this purpose it has been convenient to regard each gene as the inherited basis of a particular character in the adult organism. Yet such a concept as this is but a partial truth, and it is essential to discuss the real relationship of the genes to the characters before arriving at any clear understanding of the nature of variation and of its hereditary control.

One of the most important discoveries bearing upon this problem is the fact that the same genetic factor does not always have the same effect; for it was early found that the genes interact with the environment. Changes in temperature, in food or in humidity, may all influence the complex action of a gene upon the developmental processes which lead finally to the production of a given character in the adult organism. That this is true is hardly surprising, for we know how great may be the effect of the external environment upon processes of growth and differentiation.
That genetic phenomena are susceptible of exact study is due to the fact that a given gene will always have the same effect in the same environment. Alter the external environment and the effect of the given gene may be changed; restore it, and the original effect will be recovered.

It is at once evident, then, that variation in any character may be due to two distinct causes; to changes (mutations or recombinations) in the genes controlling it, or to changes in the environment affecting the action of such genes. Variation of the former type is said to be 'genetic', of the latter 'environmental'. It is useful to employ corresponding terms to describe the individuals themselves. An organism judged by its genetic constitution is called a 'genotype'; one judged by its appearance, a 'phenotype'. The phenotype, then, depends upon the expression of the genotype in a given environment. An example will make this clear.

We will choose the character already selected as illustrating the simple working of the laws of Mendel; black as compared with red facets in the eyes of the Amphipod *Gammarus chevreuxi*. In this way it will be easy to trace the connexion between the mechanism and the physiology of inheritance.

In natural conditions the eyes of this animal have black facets. It is viviparous, the young being hatched from the egg in a maternal brood-pouch, from which they are extruded after some days in a fully developed condition. Though minute, they differ but little from the adult. The eyes are already formed and the facets are of the normal black colour. If, however, the eggs are removed from the brood-pouch and developed artificially outside the mother, it is seen that the facets are at first a clear bright red. But they rapidly darken through shades of brown and chocolate until, at the time when extrusion would
normally have occurred, they become black (Ford and Huxley, 1927, pp. 113-14).

Thus when colour first appears in the facets, the eyes of the wild-type Gammarus are similar in appearance to those of the red-eyed form already mentioned as having arisen by mutation in the laboratory. But even in the latter the red colour does not always persist. Gradually, after a period of weeks or months, it may darken until, in some old individuals, the facets may be of a deep blackish brown. It has been proved (ibid.) that this change is due not to an alteration in the red colouring matter itself, but to a slow deposition of the black pigment (melanin) which is found in the eyes of normal specimens.

We see, then, that the difference between the black- and red-eyed form is due merely to the rate at which black pigment is deposited in the facets; a change occupying a few hours in the former type takes many weeks in the latter. Further, we obtain some insight into the nature of the genetic control of this character. The genes for the black and red facets in the eyes of Gammarus simply affect the rate at which a single substance, melanin, is deposited in the eyes. It is probable that such rate-factors, controlling the speed and time of onset of processes in the body, are of very general occurrence and of critical importance in human evolution (Ford and Huxley, 1927, pp. 126-32).

But it is evident that environmental conditions, such as temperature and food, which influence the growth of the animal, will also affect a process such as this which depends upon developmental rates. And, in fact, it has been proved (Ford and Huxley, 1927, pp. 124-26) that temperature influences the effect of the mutant for red eye colour in Gammarus. In the red-eyed form melanin is deposited so rapidly at 28°C that the
eye becomes approximately black in twenty days, while at 13°C. only a minute quantity is laid down after many months, and the eye remains bright red. At 10°C. it is even possible to delay melanin deposition that the facets of the normal black-eyed form are still quite red at extrusion from the brood-pouch. It has also been shown (Pfeil, 1928) that if growth is delayed either genetically or environmentally, in a red-eyed Gammarus, the quantity of melanin produced in a given time has to be shared out over a smaller area in the facets. Therefore, if kept at a high temperature, the genotypically red eye of such an individual can for a time become completely black and indistinguishable from the genotypic black eye of the wild-type animals.

The distinction between these two types of variation will now be plain. A character may vary when the genes controlling it are kept constant and the environment altered, as does the colour of the facets in genotypically red-eyed Gammarus, which may be made phenotypically red or black environmentally. It may, on the other hand, be varied genetically by keeping the environment constant and altering the genes which control it, as may be done by appropriate matings, bringing in the black or red factor and keeping the individuals at a low and constant temperature.

In fact, it may be said that all characters are the combined results of genes acting in a given environment. Alter either the genes or the environment and variation may ensue. The genes do not stand for this or that character in the adult organism; it can only be said that in a particular environment they will always have an identical result. Such an assumption is the logical outcome of all that is known of genetic action.
It seems that genes whose action is easily influenced by the environment are found in all groups of animals and plants which have been the subject of genetic research. Two examples out of many may be cited from the work on Drosophila melanogaster, as illustrating different types of environmental effects. A single recessive factor causes the reduplication of one or more of the legs. Sometimes only a few joints are affected, but at others all the legs may be doubled even down to the base. This factor only produces an effect at low temperatures. When the flies are reared in an ice chest, normal segregation is obtained in crosses with the wild type, but at higher temperatures, say 23° C., it is quite without effect even in the homozygous condition (Hoge, 1915). Similarly, 'abnormal abdomen', a semi-dominant sex-linked factor, results in a more or less complete obliteration of the regular banding of the abdomen. This character is fully expressed in cultures obtained from freshly made-up stock bottles. It becomes less pronounced in the flies which hatch later, until, in old cultures, all are completely normal, even the homozygous females. The abnormal effects are, however, once more obtained in full when the offspring of such phenotypically normal but genotypically abnormal flies are reared in a fresh culture medium. It has been found that moisture is the necessary agent for evoking the action of this gene; when the cultures dry up it can operate no longer. Both changes in temperature and in the acidity of the culture media have been excluded as causative agents (Morgan, 1915). Such instances as these might be greatly multiplied.

Among plants, the interaction of genetic factors with the environment may be illustrated from Barley, in which Collins (1927) detected the unusual condition of a
viable albino. This is due to the action of a single recessive factor, but it can only produce the completely albino type when the plants are grown below 6.5°C, while above 18°C they develop the full amount of chlorophyll and cannot be distinguished from normal plants. However, instances of the operation of the same phenomenon are, in reality, constantly provided by the varied response of plants to growth in different situations. The effects of alterations in soil and climate are too well known to require illustration, but they demonstrate the reaction of the plants' hereditary outfit to environmental changes.

It is evident, however, that some characters may have a fairly wide range of tolerance for environmental change. We cannot in advance predict without experiment that a given alteration in the environment will affect the action of a particular gene. In fact it is possible to regard genetic factors as having characteristic effects. So much so that in the past many workers have fallen into the trap of identifying, in some measure, the genes with the characters they normally produce, an error which has done much to obscure the interpretation of genetic phenomena.

That such a point of view should be possible is due to the fact that all organisms have an optimum environment in which they are most efficient. To this they are often so accurately adapted that it is impossible for them to live in other surroundings; while animals, at any rate, may positively seek out the right conditions, or maintain them by a physiological control by which they create a permanent and constant environment for themselves. It happens, then, that we are generally studying the action of genes in an environment close to the optimum; one which is therefore fairly constant. So it comes about that the interaction of the genes
with the environment may be by no means evident; nor can it always be demonstrated, for quite a small departure from optimum conditions is fatal to many organisms.

To take an excellent example. Temperature is one of the most obvious and important of environmental factors; we have already discussed how it may interact with a gene and affect a character in the adult organism. That each animal has an optimum temperature, which may differ widely in different forms, is a fact too well known to require emphasizing. Some species will tolerate a considerable range of temperature on either side of their optimum, to others a minute departure from it is fatal. Typical of the latter group are the Mammalia, which maintain their temperature permanently at optimum level and consequently, in this respect, live in a constant environment from which they cannot normally be dislodged. Yet we have reason to think that many of the genes in this group only produce the effects known to be characteristic of them because they always operate at this particular temperature. Indeed in a few instances at least the change of temperature necessary to influence the character produced by a gene is so small that it can be detected even here.

Himalayan rabbits differ from the wild form by a single factor-pair, the Himalayan colouring being recessive to the ordinary brown agouti. This factor is responsible for the production of a white coat at the Mammalian optimum temperature. At a temperature a few degrees lower, its action is entirely different, for it no longer produces white but black hair. Himalayan rabbits are born uniformly white, for the whole body has been maintained at a high and constant temperature before birth. But subsequently the
extremities, the ears, muzzle and feet, which are subject
to chilling, turn black; for these parts are cooler than
the rest of the body and this difference is sufficient
totally to alter the effect of the Himalayan factor.
That the darkening of this race is the result of tem­
perature has been proved in the following way. If a
patch of hair be shaved off the back of two Himalayan
rabbits and the one be kept in a warm and the other
in a very cold place, the hair which grows again will
be white in the former environment and black in the
latter (Schultz, 1920; Castle, 1924, pp. 218-19).

2. THE INTERNAL ENVIRONMENT

It is seen, then, that the genetic factors interact with
the environment to produce the characters for which
they are responsible. But the environment is not only
external but internal, and by the internal environment
is implied the total effect of the genetic constitution
of the animal. The means by which this can control
the chain of reactions from a particular gene to a
particular character, so as to produce variability, must
now be briefly sketched.

The essential of Mendelian inheritance is its particu­
late nature. This, of course, refers to the behaviour
of the genes as individual units, it does not refer to
the characters, for a single character is the result of
the interaction of many genes. There are, in fact,
unit factors but not unit characters in heredity.
Factor interaction, then, is a matter of fundamental
importance in the study of genetic action. Its recog­
nition dates from the well-known observations of
Bateson and Punnett (1905; and 1906, pp. 11-16)
on comb shape in fowls. These authors found that
the rose and pea combs were each dependent upon a
single factor which behaves as a dominant to the normal single comb. When brought together they interact to produce a new type of comb called 'walnut', which is therefore due to the interaction of two factors each having a different and characteristic effect by itself. Instances of this kind are now numerous in the literature of genetics.

Of a slightly different nature are those characters dependent upon the operation of several factors with similar but cumulative effect. Nilsson-Ehle (1909), working on the inheritance of red and white colour in wheat grains, found that red was incompletely dominant in the F1 generation and that all shades appeared in F2, from whitish to a nearly full red. His results led him to formulate the concept of multiple factors, which he developed with conspicuous success; they are now recognized as a general feature of genetics. A simple instance is that of the genes 'Stubbie' and 'stubbloid' in Drosophila melimogaster studied in detail by Dobzhansky (1930b). The former is heterozygous, being lethal as a homozygote, and the latter recessive. They control the same characters and reinforce each other.

The class of 'modifying factors' presents a somewhat different type of factor interaction. Many of these have no detectable effect save in the presence of some particular gene.

Bridges (1919) made a study of a number of such factors which modify the character 'eosin eye'. This depends upon the action of a sex-linked recessive, one of the series of multiple allelomorphs at the white-eye locus; it changes the red eye of the wild-type Drosophila to a yellowish pink, of a somewhat lighter shade in the female than in the male. In the presence of this gene the factor 'cream 2' can easily be detected, since it interacts with it to produce a marked lightening
in eye colour, which becomes a pale yellow destitute of any trace of pink. In ordinary circumstances, however, "cream 2" has no visible effect even in the homozygous condition.

'Esin eye' has a somewhat lower viability than normal, and it is improbable that it could establish itself in nature. But a striking example of modifying factors operating in natural conditions is to be found in the butterfly *Papilio polytes*, as was demonstrated by Fryer (1913). The female of this insect has three forms. One of these, known as *cyrus*, closely resembles the male, and a dominant factor converts it into the widely different typical form *polytes*. There exists another dominant which is without effect in the *cyrus* constitution. It interacts, however, with the *polytes*-producing factor to give rise to a third distinct form called *romulus*.

These two factors are *sex-controlled*, that is to say they can only produce the characters for which they are responsible in the internal environment provided by one of the sexes. In the other, in this instance the male, they are without effect; their relationship to sex is therefore of a physiological nature. Such factors may be situated in any of the chromosomes. They are thus to be distinguished from the sex-linked type (p. 14) whose relation to sex is of a purely mechanical kind, since they are carried in the same chromosome as those for sex and are, in consequence, linked with them. It is, of course, possible for factors to be both sex-linked and sex-controlled.

Essentially similar to the modifying factors is an obscure type of factor interaction, which has been encountered on a number of occasions, and may be illustrated by the work of Wexelsen (1928) on the occurrence of extra spermathecae in *Drosophila melanogaster*...
He was able to demonstrate that this peculiar reduplication is due to the combined action of at least three pairs of factors, situated in different chromosomes, each of which is without visible effect by itself.

It is apparent that the factors most convenient for genetic study are those which in the normal environment give rise to some well-marked character. This may in reality be but one of several quite evident effects of the factor in question, but, being the most obvious, it comes to be regarded as the primary one and the others as secondary. That the existence of these secondary effects is in reality a widespread phenomenon is evident from the large and increasing number of instances in which they have been detected. They have on several occasions been the object of special study, notably by Dobzhansky (1927), and they may affect any organs of the body quite independently of the primary character. Thus the factor for white eyes in Drosophila is responsible also for a change in the colour in the testis-sheath and for a characteristic alteration in the shape of the spermatheca. The white-eye character is merely selected as being the most convenient indication of the presence of this particular gene.

Even more important for the present purpose is the marked influence of mutations on viability. That this is nearly always of an unfavourable kind will be a matter for discussion in the next chapter. It is at present sufficient to notice its existence. Of the hundreds of mutations which have, for example, been studied in the various Drosophila species, scarcely one has been found which does not lower the viability as compared with the wild type, and many are actually lethal as homozygotes. Such a result can hardly ever be accounted for by the nature of any observable struc-
nccal changes. It indicates that the effects of a gene are far more profound than a study of the visible characters would lead us to suspect. In reality they must include physiological and other reactions which can only be detected by their influence on the general health and vigour of the organism. The almost universal nature of such changes in viability justifies us in assuming that the genes are probably always multiple in their effects.

It is to be noticed that the mere observation that a particular gene has manifold results does not exclude another explanation. Theoretically it is possible that there are in reality as many separate mutations, linked so closely that crossing over between them is virtually impossible, the whole group therefore being inherited together. That such an assumption is not generally tenable can be proved in those instances where the same mutation has occurred more than once. Not only the primary but also the secondary effects have then appeared again: a statement unaffected by the existence of numerous genetic units within a gene, when considered as a cistron, these being non-complementary.

The interaction of the genetic factors to form an internal environment will now be apparent. It is evident that the effect produced by any gene will be altered if another controlling the same character is introduced. The truth of this statement is evident in ordinary factor interaction, but it is obvious that it must have a wider application in view of the multiple effect of single genes. For the number of factors in any given species must be very great and if, as the evidence indicates, each controls several characters, and influences the general physiology of the organism, the whole body must be bound together by an interacting system. The influence of any one factor on the
whole may be slight, but all must combine to form a gene-complex providing an internal inherited environment varying from individual to individual. In such an environment, then, every gene has to act. As it is variable, it is evident that the effect of a given gene may be changed, even in a constant external environment, but not the gene itself.

This principle is responsible for a phenomenon very common in genetic work, that of the improvement in viability of a new mutation after several generations of inbreeding. Those individuals having a gene-complex with which the gene in question reacts in a particularly disadvantageous way are removed by selection. Of a similar nature are such instances as that worked out by Timofeeff-Ressovsky (1927b) on 'radius incomplectus' in Drosophila funebris. This character is due to a single factor; yet it was possible to establish true-breeding stocks in each of which its expression differed, owing to its reaction with a selected gene-complex.

The integrative action of genetic factors may, however, be demonstrated more clearly by the behaviour of such a gene as that producing the 'eyeless' character in Drosophila melanogaster. This is a recessive carried in the fourth chromosomes. Its effects are variable, but the eyes are considerably smaller than normal and they may be absent. By selection it has been possible to produce a stock in which most of the flies are without eyes. If, however, an unselected stock, homozygous for the eyeless factor, be inbred for several generations, practically all develop normal eyes. Further inbreeding shows that the modification which has been produced is permanent, and is not the result of temporary changes in the external environment (Morgan, 1929).
This remarkable result is susceptible of two explanations. Either the eyeless factor itself has changed, or the response of the animal to the eyeless factor has changed. It is easy to decide which of these is correct.

If the now highly inbred stock be outcrossed to ordinary wild-type flies, it is found that the extracted recessives which appear in the F2 generation have returned to the original condition. A high proportion of them show the eyeless character in an extreme degree. Thus it is evident that the gene itself must have remained unaltered, for it is capable of exercising its former effects when restored to the original internal environment as supplied by the wild-type flies.

It is clear, then, what has taken place. Among the thousands of genes possessed by the original stock, some would be heterozygous. Recombinations would therefore be possible among them, giving an internal environment differing somewhat in the various individuals. And it is to be noticed that inbreeding, such as that to which the flies were subjected, tends to produce the homozygous condition and so brings hidden recessives into operation. The eyeless gene is thus placed in a number of internal environments, with which it would react in varying degree. But the population competes for food, and in other ways, in the stock bottles. Selection would thus occur, tending to preserve those flies whose gene-complex brings out to the smallest extent the undesirable effects of the eyeless factor; for this is responsible also for a lowering of vitality and a marked reduction in the number of eggs laid. These effects would in this way gradually be diminished, and flies with practically normal eyes would appear in increasing numbers.
But it is expressly to be noticed that the internal environment is inherited. The stock would be purged by selection of those factors which bring out the maximum effect of the eyeless gene. As long as the inbreeding is maintained, the phenotypic modification would thus persist. On outbreeding, the normal gene-complex would in part be restored, carrying with it factors which intensify the action of the eyeless gene. Thus the original eyeless condition is recovered when the flies homozygous for this gene segregate out as extracted recessives in the second hybrid generation. The range of variation among them is, however, somewhat increased, owing to the segregation of other factors as well as of the eyeless gene itself.

This example shows very clearly how the gene-complex provides an internal environment controlling the effects of individual factors.

3. SUMMARY

Genetic factors interact with the environment to produce the characters for which they are responsible. But the environment is both external and internal. The external environment represents the total effect of the conditions in which the animal lives; the internal environment is due to the interaction of the whole gene-complex. Alter either the external environment or the gene-complex and the effect of a given factor may be changed. That factors on the whole tend to have characteristic effects is due to the circumstance that every animal has an optimum environment. This it endeavours to maintain as closely as possible, so that the conditions in which factors operate are generally fairly constant.

We have, therefore, no knowledge of the effect of
individual factors. All that can be said is that a given factor will evoke certain characters in a particular external environment and in the presence of all the other factors of the organism.
CHAPTER III

EXPERIMENTAL GENETICS AND ITS BEARING ON EVOLUTION

In the earlier years of this century, any attempt to apply the results of experimental genetics to the study of evolution generally provoked a storm of criticism. Among numerous theories of inheritance, Mendelism alone stands out as susceptible of proof and of exact study. Its operation has been demonstrated in the most diverse groups of living organisms, and it is known to be responsible for the great bulk of hereditary variation. Yet it is to the application of this theory that so much exception has been taken. It is a matter of great importance, then, to examine why the value of so imposing a body of facts as that presented by the Mendelian phenomena should seriously have been called in question when applied to the solution of evolutionary problems.

It must at once be obvious to anyone who has given the matter attention that many of the characters studied by geneticists do in fact differ fundamentally from those which appear to be responsible for evolutionary progress in nature. It will be valuable to consider this criticism in detail and to determine in how far it is justified.

1. THE PHENOTYPIC EFFECTS OF MUTATION

It may be said that all genetic factors which have arisen by mutation in the laboratory have certain
peculiarities in common. It seems that they are nearly always associated with some lowering of vitality as compared with the wild-type form, and the more marked their effect the more deleterious seems to be their action. They appear to be concerned with the production of small superficial differences or with obviously pathological departures from normality which could not in any event survive in a state of nature. Further, nearly all are recessives. A few so-called dominant mutations have certainly occurred in Drosophila and other forms, but these do not in the least represent the production of normal dominant characters such as the wild-type allelomorphs of the recessive mutations. For such genes, though exercising an effect in the heterozygous condition, are not completely dominant and are usually found to be extremely lethal as homozygotes. Indeed, in the majority of such instances the homozygous type is wholly inviable.

There is, then, a sharp distinction between the normal dominant factors found in nature and the recessive genes which arise in the laboratory, a distinction which is emphasized rather than obliterated by occasional dominant mutations, for these generally seem to produce characters of an exceedingly lethal description. It may, in short, be stated that no mutation has ever occurred in the progress of genetic work which is fully viable and behaves as a dominant to the wild-type condition. That any have given rise to changes which could be of survival value in nature appears highly doubtful. It is just possible that in one or two instances they might be of advantage in special circumstances, but this is at any rate quite exceptional. It may legitimately be inquired, therefore, whether the results of genetic research based upon the behaviour of such
It is, of course, to be noticed that many instances in which variation is controlled in a Mendelian manner have been detected in animals and plants both in natural and domesticated conditions. But it must be remembered that the mutations which occur in the laboratory have provided the material on which most of the important experimental work has been based, and that these are nearly always deleterious and generally recessive. There are, however, two considerations which place this fact in a new light and indicate that the study of experimental genetics has, after all, a direct bearing upon the problems of evolution. Firstly, it can be shown that disadvantageous mutations must in all circumstances be much more frequent than those of a favourable kind; secondly, that a tendency seems to exist for all disadvantageous mutations gradually to become recessive, while those which confer any benefit on the organism will progress in the direction of increasing dominance until they are incorporated in the normal gene-complex, the former wild-type genes being converted into recessive allelomorphs.

These points must be examined more minutely. It is to be observed that mutation is not directional. There is no evidence that any particular circumstances cause certain genes to mutate, nor does the quality of a gene change at a particular locus appear to be anything but purely fortuitous. On the other hand, it has already been shown that the genes are intimately related in function, inasmuch as they form an interacting gene-complex whose results in a given environment have been selected as beneficial to the species. The chances, then, are small that any random change in this balanced system should fit in with the
delicately adjusted machinery of the gene-complex so as to produce harmonious working. Considered in this light, mutation would be expected most often merely to upset the normal balance of development and produce a lethal effect. Even if it happened so to fit in with the arrangement of existing genes as not to imperil the operation of the whole, the chances are probably extremely remote that the effect thus produced would be of advantage to the organism.

Quite evidently, the more pronounced the changes involved by a particular mutation, the greater are the chances that it will produce an undue disturbance in the existing system. If this is already a very complex one, such a disturbance is even more likely than if it is of a simpler kind. We may therefore anticipate that beneficial mutations will most often involve changes of small magnitude and that they may perhaps be less frequent in highly adapted than in unspecialized organisms.

Some of these considerations have been subjected to an exact mathematical analysis by R. A. Fisher. He has demonstrated the low mutation-rates of beneficial mutations in an argument of much interest, based on the chance of survival of a single gene. For further information on this point reference should be made to this study (Fisher, 1930b, pp. 70-83).

It will thus be seen that advantageous mutations are in all circumstances probably very rare indeed. On general grounds they might be expected to occur perhaps once in $10^5$ individuals. At any rate, their frequency may be something of this order. Nearly all genic changes therefore will be of a disadvantageous kind, and it is necessary to discuss in what way the organism will react to them.

The possibility that dominance is arrived at by
selection operating on the gene-complex has been de­
veloped with much success by Fisher (1928 a and b,
1929). Briefly this theory may be outlined in the follow­
ing way.

It is known that mutation is a recurrent phenomenon.
In Drosophila mutations at the white-eyed locus have
certainly occurred spontaneously more than thirty
times and similar, though generally less frequent,
repetitions have been observed at other loci, and in
various species both of animals and plants. It is
not known what relation the mutation rate in nature
bears to that under experimental conditions, though
mutations such as those observed in the laboratory
certainly occur naturally. For instance, the first gene
to be discovered in Drosophila simulans was that for
yellow body-colour. It is a sex-linked recessive, and
was found by Metz in a wild specimen obtained in
Florida (Sturtevant, 1921, p. 44). It has been proved
to be identical with the gene for yellow body-colour
in Drosophila melanogaster (ibid., p. 47). Gerschenson
(1928) detected a sex-linked, and sex-controlled, factor
in Drosophila obscura in natural conditions. Its effects
are confined to the male and are purely lethal, since
it prevents the formation of nearly all spermatozoa
bearing the Y-chromosome and gives rise to a sex­
ratio of about 96 females : 4 males. Such genes as
these are of a type quite similar to the disadvantageous
recessives which arise by mutation in the laboratory.
Furthermore, the studies of Dubinin and his collabora­
tors (1934) on Drosophila melanogaster, and of Dobzhansky and
Queal (1938) on D. pseudo-obscura, have demonstrated
that recessive genes in the heterozygous state are widely
spread in wild populations of these species. Similar
evidence is also accumulating for other organisms.

There can be no doubt that in every species the
total number of individuals breeding in a single year must greatly exceed the total number ever subjected to genetic analysis; this must be true for *Drosophila melanogaster* of which, astonishing as it may seem, a million or more have been bred and examined under experimental conditions. We may feel confident, then, that few if any of the mutations which have occurred in the course of genetic work are in reality novelties. The species must already have had a long experience of them and have been able to adjust itself to them, if in fact any such adjustment is possible. The strong probability that it is will be apparent in view of the interaction of the genes with the internal environment which has already been outlined.

It is normally to be expected that two doses of a gene should be more efficacious than one, so that when a mutation occurs for the first time in the history of a species we may fairly assume that the resulting heterozygote will have an effect intermediate between that produced by either homozygote; of this there is some evidence, as will shortly appear. So long as a gene is rare in the population it will occur vastly more often in the heterozygous than in the homozygous state. For in such circumstances the chances of two heterozygotes mating will be remote; far more often a heterozygote will mate with an ordinary wild-type individual, and the new gene will be passed on to half the offspring, once more as a heterozygote. Clearly, then, the reaction of a species to any really new mutation will be adjusted to the effect which the resultant gene produces in the heterozygous state.

Now the gene-complex is not constant even in nature. It varies owing to a certain amount of heterozygosity, which allows recombinations of factors to take place. A new gene will thus be placed in a number of different
internal environments, with which it will react to a varying degree. Should its effects be of a disadvantageous kind, selection will favour those combinations of factors which bring them out to the smallest extent. There will thus be a constant tendency operating to modify the reaction of the species in such a way that the effects of a disadvantageous gene will be masked in the heterozygote, so leading to recessiveness. This process is, in fact, quite comparable to that already described in such instances as the eyeless character in which the disadvantageous phenotype was proved to be obliterated by selection of factors forming the internal environment. The only difference is that we were then dealing with the production of recessiveness in the homozygous instead of in the heterozygous condition.

Ultimately, when the recessive state has been attained, a similar but even slower process favouring the obliteration of the disadvantageous effects of the homozygote might be expected to take place. This should end in the gene ceasing to have any effects at all in normal circumstances. If, however, another mutation controlling similar characters were to arise, such an old and ineffective gene might show itself as a 'specific modifier'. Consider, for instance, an allelic pair controlling the rate at which pigment is produced in the body, such as the factors for the production of black and red facets in the eyes of Gammarus. If the wild-type allelic form (the dominant black factor) of such a pair produces pigment up to saturation value very quickly, any small effect left to a similar mutation, which had been subjected to long-continued counter-selection, would be undetectable. Such a gene might, however, still have the opportunity of exerting some effect if pigment production were greatly delayed by some other factor, such as that producing the red eye.
For the facets then remain for a long time in a sensitive condition in which it is possible to observe very small changes in the rate of melanin production. In this way certain factors might come to have an effect only in the presence of a particular gene. These have already been mentioned in Chapter II, and their presence has also been demonstrated in the instance discussed here. For it has been shown (Ford and Huxley, 1927, pp. 115-23) that there exist more than one pair of factors affecting, to a very slight degree, the rate of melanin deposition in the eyes of *Gasteria*. This they do in a manner quite similar to that of the pair responsible for the major control of this process. Their effect, however, is so minute that they can only be demonstrated in the slowly darkening red-eyed condition, produced by the retardation of melanin development. The origin of such 'specific modifiers' has long been a matter for speculation, as the occurrence of genes solely concerned in modifying others, which are themselves evidently incapable of becoming established in nature, has seemed difficult to explain. It appears, however, that they may be the result of long-continued counter-selection acting on a disadvantageous mutation in the manner here outlined.

In the rare event of a beneficial mutation, a process the reverse of that so far described would take place. The gene-complex which brings out the effects of the heterozygote to the greatest extent would be selected, and the new mutant gene would become dominant to the original wild-type allomorph, which it would automatically supplant.

The effects of the more markedly lethal genes must, on the other hand, be uninfluenced by selection. The individuals carrying them will be at such a disadvantage that they will generally be killed off whenever they
appear, and there will be no opportunity for selection of the gene-complex to take place in respect to them. To this class, no doubt, belong the rare semi-dominant and highly inviable mutations which occur from time to time in genetic work. They will have left too few descendants to have modified much the reaction of the species to them, even as heterozygotes.

Thus it is not to be expected that completely dominant genes having new and advantageous effects should appear as mutations in genetic experiments. Complete dominance is probably the result of selection accentuating the effects of an initially beneficial heterozygote, and a gene of this kind should be quickly incorporated in the wild-type constitution. The production of dominance in a new favourable mutation should be a far more rapid process than the corresponding drift towards recessiveness in a disadvantageous gene, which is continually being extinguished by counter-selection; for this can only be brought about by recurrent muta-

It will be seen that on the theory here outlined dominance is to be regarded as one of the phenotypic effects of a gene. It is to be expected, therefore, that it will be susceptible to such modifications as affect the other manifestations of genic action. We may now discuss a few of the facts which support this point of view.

Consider first the action of the external environment. It is perhaps hardly to be expected that once the completely recessive condition has been established, external changes within the toleration of the species should be capable of restoring marked phenotypic activity to the heterozygote. For the fact that counter-selection may continue to act upon the homozygote will always tend to reduce the effects of disadvantageou
MENDELISM AND EVOLUTION

32

genes beyond what may, in normal circumstances, be the bare minimum necessary to inhibit them in the heterozygous state. Small variations produced by changes in the external environment would probably therefore not be detectable, though they might be where the production of complete recessiveness has not been attained. Instances of this kind have, in fact, been observed. For example, the bar-eye factor in *Drosophila melanogaster*, which is an incomplete dominant, reduces the number of facets in the eyes and its effect can be expressed quantitatively. Hersh (1924, 1927) found that the degree of dominance of this character varies with the temperature at which the flies are bred.

The chief interest, however, attaches to the modification of dominance due to changes in the internal environment. The important general effects which such changes produce upon the action of genes have already been discussed in Chapter II. It will therefore be necessary only to mention here certain instances which throw special light upon the origin of dominance.

Fisher (1930) has already drawn attention to the relevant behaviour of the 'crinkled-dwarf' factor which arose as a mutation in Sea Island cotton. In this species it is a simple recessive, while in the other New World cottons it has not been observed. It can, however, be introduced into them by crossing. This has been done by Dr. S. C. Harland, who finds that crinkled-dwarf is no longer a recessive in the F1 plants, while in F2 every degree of dominance seems to appear, giving apparently continuous variation. It is evident, therefore, that the gene-complex of the Sea Island cotton is so adjusted as to inhibit the effects of the crinkled-dwarf factor in the heterozygous state, while
no such adjustment has taken place in the species unaccustomed to this mutation.

Somewhat similar evidence may be obtained from a consideration of the various effects of a single gene. Dobzhansky (1927, p. 383) has shown that the allelic factors at the white-eye locus, and the wild-type, sooty, and ebony body-colour series in Drosophila, have a secondary effect on the shape of the spermatheca. They produce small but exceedingly constant changes in proportion which are practically uninfluenced by external conditions, which, however, alter the absolute size of this organ very considerably. It is difficult to see that such changes as these can be controlled by direct selection. On the other hand, body-colour, or eye colour in so far as it can influence the efficiency of vision, must be of direct importance in the insects. It is therefore a striking fact that while the genes controlling these characters are completely recessive in so far as their external effects are concerned, yet in the shape of the spermatheca the heterozygotes are intermediate. It would appear that selection has been able to produce the recessive condition in respect of disadvantageous characters, without influencing their harmless secondary effects.

It has been suggested, then, that selection of the gene-complex in respect of particular factors may take place in two ways; first, by favouring the action of one rather than the other allelomorph in the heterozygote, and later by the obliteration of the effects of a gene even in the homozygous condition. It will be a crucial test, therefore, to examine the reaction of factors when balanced against each other in combinations such as cannot previously have occurred, or have at any rate been of such excessive rarity as to have left no impression upon the species. It is evident that such
combinations as these can be provided by the multiple allelomorphs.

A number of different changes at the same locus may each occur as mutations. These will of course be very rare, and each will therefore find itself in competition with the wild-type allelomorph, since, as previously pointed out, in rare genes the heterozygote is immensely commoner than the homozygote in wild populations. As such genes will nearly always be disadvantageous they will be prevented from spreading widely. It is evident, therefore, that the chances are almost infinitely remote that two different mutant members of the same series of allelomorphs can find themselves in competition with each other in natural conditions. Now the reactions of multiple allelomorphs are well known in a number of forms. It has been found that though in general each behaves as a simple recessive to the wild-type gene, when the two members of such a series are brought together by experimental crossing, the heterozygote so formed is intermediate between them. This relationship seems to exist in all the instances studied; it occurs in the most diverse forms, for example in Drosophila (Morgan, Bridges, and Sturtevant, 1925, pp. 34-6) and Rodents (Feldman, 1924). It is plain that this provides a very important corroboration of the theories discussed in this chapter, for it shows that a condition of dominance and recessiveness has been established between such factors as can normally have been in competition, but not between two factors which probably have never been brought together before.

Certain objections can be raised to the efficiency of such selection as is here described. Of these the most important is the contention that it is not sufficiently powerful to produce an effect except in artificial conditions, owing to the rarity of heterozygotes in nature.
This view has been supported on mathematical grounds by Sewall Wright (1929 a and b). Fisher's calculations (Fisher, 1929), published in answer to those of Sewall Wright, would seem to indicate, however, that it must be a factor of importance. It has indeed now been possible to produce dominance-modification experimentally in a wild species, the Currant Moth Abraxas grossulariata. The variety lutea, which converts the ground-colour from the normal white to yellow, has an intermediate effect in the heterozygous state. By selection of the more and of the less extreme heterozygotes respectively, it has been possible to make this variety almost a dominant in one line and almost a recessive in another (Ford, 1946).

It may further be doubted whether the gene-complex is capable of modification in many directions at once, as is required for the adjustment of the numerous mutations which occur from time to time. But, in the majority of instances the alteration in the phenotypic effects of a gene will probably be brought about principally by selection operating on comparatively few factors; generally those which are concerned in controlling the same characters, or at any rate the same developmental effects, as the gene in question.

An interesting alternative suggestion of the manner in which dominance may be attained has been made by J. B. S. Haldane (1930). He draws attention to the strong probability that many genes may act up to a saturation value beyond which no effect can be obtained. Now it is clear that any mutations occurring in a gene which has reached saturation level can only be detected if they take place in a minus direction and, in consequence, a number of phenotypically inseparable mutations of higher value might become available for recombination. Haldane suggests that those hetero-
zygotes will be selected in which less mutations are balanced by allelomorphs so much above saturation level that the combined action of the pair is not reduced below it. Thus there would be no reduction in activity in the heterozygous condition, and dominance would result.

It will be seen that on this view dominance is also brought about by selection, but that this is assumed to operate on multiple allelomorphs rather than on the gene-complex. Now there is good reason for supposing that in many instances the genes do in fact set up to a saturation value. In wild-type *Gammarus* the factor controlling melanin deposition is certainly responsible for the production of more pigment than is necessary to make the facets black. As already pointed out (p. 30), a recessive gene inducing melanin formation in relatively small quantities can produce complete blackening before the facets have increased in size. In larger eyes, however, the amount of melanin may not be sufficient wholly to obscure the red pigment. It is evident, then, that in some environments reduction in the activity of the melanin-producing factor in *Gammarus* could take place without producing detectable effects. The same conclusion is arrived at by the important work of Stern (1929), who was able to build up the normal dominant condition in *Drosophila* by accumulating the recessive multiple allelomorphs of the character 'bobbed' (bb) carried in extra Y-chromosomes. It is apparent, then, that the amount of genic material present at a locus can have a quantitative effect and, where this acts up to a saturation value beyond which the phenotype cannot be altered, complete dominance will result, provided that this value is exceeded in the heterozygote.

It has, however, been pointed out (Ford, 1930) that
such saturation levels cannot be regarded as fixtures inherent in the species, but they must be determined by the activity of the organism as a whole. They must therefore respond to changes in the gene-complex, so that selection of the type postulated by Fisher may none the less be the primary factor controlling dominance even where selection of particular multiple allelomorphs takes place in the manner suggested by Haldane.

Although, as we have seen, the occurrence of new mutations immediately ousting the wild type is not to be anticipated, reverse mutations from a recessive gene back to the normal allelomorph have been known to take place. This would be expected if the wild-type characters were originally due to such mutations as occur in experimental work, but not if these latter are an abnormal phenomenon playing no part in the evolution of species in natural conditions.

All instances of apparent reverse mutation must be critically examined, as it cannot always be proved that the appearance of a normal individual in a stock homozygous for some recessive gene is not due to the accidental introduction of a wild-type specimen. In certain instances, however, this possibility can be excluded. Thus Timofeeff-Ressovsky (1927a), working on "radius incompleitus" in Drosophila funebris, discovered a normal fly in a homozygous stock after twenty-four generations of inbreeding; on testing it was found to be heterozygous, and consequently could not have been accidentally introduced. The radius incompleitus factor is not always phenotypically expressed; but such apparent returns to normality had often been tested, and on all previous occasions had proved to be genotypically pure. Shisan Chen (1928) obtained an autosomal mutation producing "transparency" in the course
of his studies on gold-fish. He also obtained somatic mutation of the normal to the transparent gene and the reverse. Other instances might be cited. One which illustrates an important genetic situation is the mutation of the gene for miniature wings in *Drosophila virilis* studied by Demerec (1926, 1929 a and b). This often reverts to the wild-type allomorph, and the frequency and type of mutation, whether germinal or somatic, is partly controlled by other genes.

Of special interest is the fact that reverse mutation from a recessive gene back to the normal allomorph has been produced by X-rays (see, for example, Timofeeff-Ressovsky, 1929, and Patterson, 1929). For it has been maintained that the induction of mutation by this means is to be regarded as proof that recessive genes are abnormalities, since they can arise when, as it is suggested, damage has been done to the germ plasm by a source of destructive nature. Such a conclusion is seen to be untenable. If some mutations represent damage to the chromosomes, others represent the repair of this damage; the agent which in one case produces the wound is the same which heals it in the other.

2. **Domestication**

As so many genetic problems have been studied on domestic animals and plants, it will at this point be convenient briefly to consider the effects which the peculiar conditions to which they are subject have on the phenotypic expression of their genes. Not only are domesticated species protected from rigorous selection, but types actually disadvantageous in natural conditions may be favoured by man, either for special purposes or merely as curiosities. For this reason many of the genetic factors found in domestic species...
differ considerably in their behaviour from those so far described.

It has been pointed out that in *Drosophila*, and other forms used in laboratory experiments, mutations give rise either to recessive genes or to imperfect dominants, usually of a very lethal description. Yet in domesticated species it is quite common to find healthy varieties produced by genes whose effect is detectable in the heterozygote. Such viable imperfect dominants or recessives are known in cattle, sheep, horses, dogs, cats, rabbits, guinea-pigs and other forms. It is often extremely doubtful, however, if such varieties could survive in natural conditions. We may suspect that the genes which are now responsible for them have been arising by recurrent mutation in the past, and that they were constantly being eliminated by selection, leading to complete dominance of the wild-type form.

Such recessive mutations would be seized upon as novelties during domestication and preserved. Those individuals in which their effects were most apparent would be used for breeding, and the type accentuated by a selection of the gene-complex the reverse of that which had proceeded in nature. In this way many of the mutations might be brought back to a state in which the heterozygote is affected. Such artificial selection would of course be extremely rapid compared with the corresponding process in nature. Once a distinct difference had appeared, the heterozygous form, rather than either homozygote, seems to have been especially valued in certain instances; as perhaps the red-roan coat colour in Shorthorn cattle, and certainly the 'blue' plumage in Andalusian fowls. Here the change would be even more speedy and profound, for no attempt would be made to select the gene-complex in such a way that either homozygote
should approach the desired form. The most valued individuals would naturally be bred from, so that direct selection would take place for those heterozygotes which differ most from either homozygous type.

Finally, it may be mentioned that in poultry a quite exceptional condition is found, for some of the factors which separate the domestic breeds from the wild jungle-fowl are actually complete dominants. The dominant white plumage of the White Leghorn, and the rose and pea combs, are familiar examples. This evidently presents a somewhat different problem from that already discussed. A satisfactory explanation of it has been arrived at by Fisher (1928b). He points out that the original conditions of domestication of the poultry, which took place in Burma and apparently in northern India, differed from those of most animals; for there the flocks were, and often still are, subject to constant crossing from wild individuals. In this way the normal allelomorphs of any mutations were continually being brought in, so that selection could only proceed in favour of such genes as initially showed at least some slight effect in the heterozygote. This conclusion has now been verified by Fisher (1935, 1938). He reversed the presumed evolutional process by introducing genes dominant in domestic poultry into the wild jungle-fowl; these then exercised distinct heterozygous effects.

As soon as domestic poultry had been spread by human agency beyond the natural range of their wild representative, these peculiar conditions would no longer prevail. Recurrent mutations which had become recessive through natural selection would then stand a fair chance of being detected when they occurred in the flocks. We therefore find that numerous varieties dependent upon recessive as well as dominant factors have been established in domestic poultry.
Mutations occurring in the laboratory give rise either to recessive genes or to semi-dominants, generally of a definitely lethal description. Either type is, however, nearly always associated with at least some decrease in viability, nor do such mutations produce changes which are likely to be of advantage in nature. It appears, however, that disadvantageous mutations must be immensely more common than those conferring any benefit on the organism, and that a tendency exists for them gradually to become recessive. This is due to recurrent mutation enabling selection of the gene-complex to take place in favour of those heterozygotes which have the least marked effect. A continuation of such selection acting on the homozygote will lead to the obliteration of the phenotypic effects of a gene, except in certain circumstances in which it might act as a specific modifier. If a mutation is initially very lethal no change can, however, occur, and the gene remains as a more or less inviable semi-dominant. In the rare advantageous mutations a process the reverse of that so far described will take place; the new gene will rapidly become dominant and be incorporated in the wild-type gene-complex.

The peculiar conditions to which domestic animals are subjected lead to a mitigation or reversal of selection. This accounts for the fact that genes producing characters of normal viability, with effects detectable in the heterozygote, may be found among them. In certain instances, seemingly amenable to special explanation, the heterozygote may differ considerably from either homozygote, or varieties may actually be established which behave as complete dominants to the wild-type form.

It will be seen therefore that the fact that laboratory
mutations generally give rise to recessive genes, of a kind unlikely to establish themselves in nature, does not mean that they represent a condition fundamentally different from the production of their wild-type allelic morphs. The results of genetic research can therefore legitimately be used in the interpretation of natural phenomena.
CHAPTER IV

THE APPLICATION OF THE MENDELIAN
THEORY TO EVOLUTIONARY PROBLEMS
IN NATURE

I. MENDELM AS THE BASIS OF ORGANIC INHERITANCE

THE considerations brought forward in the last chapter indicate that the results of experimental genetics are directly applicable to the study of evolutionary problems in nature. It was seen that though the wild-type factors differ so markedly from their recessive allelomorphs, yet both may have been arrived at by similar processes of mutation and selection. Before any further use can be made of this important conclusion, it must be inquired whether we are justified in supposing all inheritance to be of the Mendelian type.

Two supplementary methods of inheritance can be suggested in opposition to this view. First, that the most fundamental part of inheritance is, in fact, maternal; it may be that the main outlines of each organism are dependent upon qualities inherent in the cytoplasm, while only the more superficial characters are controlled by the activity of the nucleus, and are in consequence supplied equally by both parents. Secondly that, in so far as inheritance is bi-parental, there may be behind the Mendelian phenomena an elusive background of blending inheritance too subtle so far to have been subjected to experimental study. These two possibilities must now briefly be considered.
The first, that inheritance may not be wholly bi-
sexual, certainly presents the more difficult problem. This theory has been revived at intervals, appearing in various guises until quite modern times (Russell, 1930). But the substantial equality between each parent and the offspring in biometrical correlations seems to exclude uni-sexual, and therefore cytoplasmic, inheritance as a phenomenon of wide application, except for those basic characters whose variation cannot be studied, and to these we shall return.

Purely maternal (Non-Mendelian) inheritance is, of course, known to occur, as, for example, the plastid inheritance which may be responsible for certain kinds of albinism in plants. Thus Correns (1900) studied a race of the Common Four-o’clock (*Mirabilis jalapa*) in which the leaves are made up of patches of green and white, while entire branches may sometimes be of one or the other colour. He showed that self-fertilized flowers on a green branch produce permanently true-breeding green plants, those on a white branch only white, while those on checkered branches give white, green, and checkered offspring in proportions relative to the amount of green and white on the branch from which the flower comes. Crosses between flowers on green and white branches give offspring which inherit the colour of the maternal branch only, whichever way the cross is made. It may, in parenthesis, be noticed that the control of chlorophyll production may also be directly Mendelian, as instanced by the work of Collins already mentioned (p. 32).

Such rare cytoplasmic inheritance as this does not, however, touch the fundamental problem with which we are concerned. The question remains to be settled whether or not the characters determining the basic development of the species, according to the phylum, class,
EVOLUTIONARY PROBLEMS

or order to which it belongs, are bi-sexually inherited. Perhaps the only definite evidence which can throw any light on this important question is to be obtained from the work on experimentally produced larval hybrids. Boveri (1903) was able to fertilize enucleated eggs of Sphaerechinus with the sperm of Echinus. He found that the skeleton of the resulting larva was purely paternal in type, so that the sperm nucleus was capable of controlling the generic characters of the skeleton in a cross between these two closely related Echinoids. Godlewski (1906), on the other hand, succeeded in fertilizing enucleated eggs of the Echinoid Echinus with sperm of the Crinoid Antedon. All the offspring died at an early stage, but in a few, development proceeded sufficiently far for gastrulae to be formed. In these it was apparent that the cleavage and mode of gastrulation was purely maternal. The sperm nucleus, therefore, though supplying the only nuclear material present, was unable to impose upon the foreign cytoplasm a course of development typical of another Class.

We see, then, that such fundamental characters as skeletal differences are controlled wholly by the nucleus in a cross between two nearly related species. The most important matter, however, is to decide what interpretation can be placed upon the result of the wider cross. Since Godlewski made no measurements of nuclear size, it has been suggested by Boveri that these supposedly haploid gastrulae came from fragments in which the nuclei were present but were invisible in the living state and, consequently, that they represented a condition of parthenogenesis through activation by the foreign sperm. If, however, the experiment can be accepted in its full force, it certainly indicates that, in this instance at least, the cytoplasm of the egg is alone concerned in determining the type of cleavage. But the cytoplasm develops...
in the presence of the maternal nucleus and gene-complex, and this may be responsible for directing the early development, perhaps before the new diploid nucleus can exercise its effect.

The strong probability of this is indicated by the work of Tennent in fertilizing the normal (nucleated) eggs of *Cidaris* with the sperm of *Lytechinus* (Morgan, 1927, p. 635). In the latter genus development proceeds much more rapidly than in the former, and the origin of the mesenchyme cells is different. In the cross-fertilized egg no effect of the sperm is observable before gastrulation begins, for the rate of cleavage is not hastened and the blastula has the appearance typical of *Cidaris*. The origin of the mesenchyme, however, is intermediate between the two parental types. In the hybrids it is not formed until after gastrulation has begun, and by that time the cytoplasmic-nuclear relation has been restored to normal. Godlewski (1925) has shown that in the Echinoderms this is usually about 7:1. In the mature egg it is 400:1, in the four-cell stage of the embryo 18:1, in the sixty-one-cell stage 12:1, while in the fully-formed blastula it has returned to its normal value.

It may well be, therefore, that the nucleus is unable to control a volume of cytoplasm relatively so great as that found in the earliest stages of development, but that it asserts its effect when the normal conditions are restored. The course of development up to that time may be determined by the maternal gene-complex. We have no clear evidence that this is so, but such an assumption is quite a legitimate one in view of the fact that instances are known in which the parental gene-complex imposes an effect upon the next generation as in gastropod torsion (Diver, 1920) and in the control of heterostyly in *Primula* (Ford, 1964).
It is thus apparent that, contrary to what might at first be suspected, the experiments of Godlewski are quite incapable of deciding the question whether or not the early stages of development are determined by purely cytoplasmic or by nuclear inheritance. The early development of the two genera of Echinoids used by Boveri is identical, no difference between them could in any event be detected until the formation of the skeleton. To this stage the offspring of Godlewski’s inter-Class cross never attained; no evidence therefore is available to show whether or not the Crinoid nucleus could affect the Echinoid egg in the later stages. Thus the two experiments are in no sense contradictory.

It appears then that, in so far as the evidence goes, the most fundamental characters are determined by the nucleus, that is bi-sexually, except perhaps those which are responsible for the main outline of development characteristic of the phylum, class, or order to which the species belongs. Even in this matter the evidence we possess is consistent with the view, established on general grounds, that such characters are in reality controlled by nuclear action.

It remains, therefore, to be considered whether all nuclear inheritance is Mendelian. It is a significant fact that though many instances are known in which crossing results in continuous variation in the F2 generation, rather than sharp segregation, yet detailed study has always indicated that the blending so produced is apparent rather than real. The interaction of several factors having cumulative effects may make it impossible to separate the phenotypes at segregation. Other complications lead to a similar condition; for example, the heterozygote may overlap both homozygotes to a greater or lesser extent. But the particu-
greater range of variation in the F2 than in the F1 generation, for this is not to be anticipated if blending were to occur. It is further supported by the fact that the more extreme forms which are recovered show at least a considerable return to one or other of the grand-parental types. The proportion in which these types themselves segregate out of a cross is, of course, extremely small if several factors are involved, and very great numbers of F2 individuals would have to be bred in order to obtain them.

Although it appears that the facts of heredity as established by experiment cannot be explained on the assumption of blending inheritance, it is obvious that this does not by any means exclude the possibility that such occurs. It may be argued that the characters controlled by this means are not of a kind which can be studied by the experimental methods so far employed. Indeed, the position of those who support such a theory appears at first sight to be a safe one; as new facts come to light, extending more and more widely the application of Mendelism, they can always retract their claims, maintaining that only characters of the most fundamental kind are subject to blending. It has, however, been pointed out by R. A. Fisher (1930, p. 18) in an argument of much ingenuity that, in certain instances at least, the possibility of blending inheritance can be wholly excluded. Only the main outlines of this demonstration will be discussed here, as detailed information on the subject can be obtained from the work in question.

It is evident that one of the most important ways in which particulate inheritance differs from any blending mechanism is in its capacity to maintain the variability of the species. With particulate inheritance the rate at which variation is extinguished is, in large
EVOLUTIONARY PROBLEMS

populations, exceedingly slow; with blending inheritance it is halved at each generation in matings between unrelated individuals, while even quite close inbreeding serves only to retard this process to a slight extent.

With blending inheritance, therefore, either uniformity must quickly be reached or else the variability must constantly be maintained by mutation. Now there can be no doubt that much inherited variation occurs among wild species, and it is certainly found abundantly among those subject to domestication. Yet, as pointed out previously, mutation is a rare phenomenon; its frequency appears to be of the order necessary to maintain variability when conserved by particulate inheritance. There can be no doubt at all that it is far too infrequent to provide the constant supply of new variation which would be required if a considerable proportion of the characters were subject to blending.

This consideration serves only to support the conclusion already reached, that Mendelism is responsible for the bulk of organic inheritance. But Fisher (1930b) has drawn attention to the fact that the work on 'pure lines', when studied from this point of view, supplies more definite information. Self-fertilization rapidly leads to a condition of homozygosity, since all factors already homozygous must remain so, while the number of heterozygous allelomorphs is rapidly reduced, half becoming homozygous at each generation. Johannsen (1903, 1913), working on a species of bean, was able to establish a number of such homozygous lines, in which hereditary variation is of course entirely absent. He showed that within such lines selection for size and other characters is unavailing even when continued for more than ten generations, although the fact that a number of different lines were established proved that heritable
variation is normally present in the species. Fisher (ibid.) points out that had any appreciable proportion of such variation been dependent upon blending inheritance, the stream of mutations necessary to maintain it would, in ten generations, have supplied it almost to the maximum degree and must certainly have been revealed by selection. Only two mutations actually appeared.

2. MENDELISM AND SELECTION

We have now reached two important conclusions; that the results of experimental genetics may safely be applied to the solution of evolutionary problems in nature, and that the great bulk, and perhaps the whole, of organic inheritance must be of the Mendelian type. These enable us to draw certain deductions from the facts so far considered. We have seen that genetic factors interact with their internal environment, and that their effects can in consequence be altered by selection operating on the gene-complex; the way in which this produces the conditions of dominance and recessiveness has already been discussed. It is evident, however, that such selection opens up another possibility of considerable importance for evolutionary theory; that the effects of a given gene may gradually alter. We have, in fact, no ground for assuming that the characters to which a particular gene gives rise are those which it produced at its first appearance. We are therefore confronted with two distinct effects of selection, which have not generally received separate recognition. First, that an inherited character conferring any advantage on the individual will tend to spread through the species, since the individuals which possess it will be favoured by selection; secondly, that the effects of a gene, if advantageous, may be intensified, and perhaps altered in quality, owing to the tendency
for those individuals to be preserved whose gene-complex brings them out to the greatest extent.

The first of these processes, the natural selection of characters, is of course familiar to all students of Biology, and has gained general acceptance. It is not seriously doubted that individuals possessing any specially advantageous quality will on the whole contribute more to the ancestry of future generations than those which fall below the average standard of the species and that, in so far as such departures from the mean are inherited, this process will lead to evolutionary change. This is pure Darwinism, and assumes no special type of inheritance. The second, the natural selection of factors, is one which follows inevitably from such facts as those discussed in Chapter II (pp. 38-42), and is the outcome of Mendelian research. It has removed some of the difficulties felt by those who hold that the principles of particulate inheritance are at variance with what is known of evolutionary progress.

These difficulties are of several kinds, but they may perhaps be grouped under three main headings. Two of these have already been discussed: that the genes appear to be chiefly responsible for the production of characters which could not be of value to the organism, and the possibility that they contribute only a part of the heritable variation of the species. The third is due to the idea that the characters controlled by Mendelian inheritance arise ready-made by mutation, to be selected or rejected in the struggle for existence as the case may be. Such a discontinuous origin of characters is, in its crudest sense, rightly felt to be inconsistent with the slow and continuous course of evolution. This objection has been stated clearly by Professor MacBride (1930), who said that the theory has been exposed by some writers that evolution proceeds by sudden jumps
or 'mutations' like the sports which occasionally turn up in the farmyard or garden, and that occasionally one of these sports, which occur for no assignable cause, 'chances' to fit the demands of the environment and survives. He continues: 'Suffice it to say that this doctrine . . . finds no countenance with those really competent to speak on the subject of evolution. Our leading systematists, paleontologists, and embryologists are all convinced that evolution has been slow, functional, and continuous.'

It is to be noticed that this criticism omits all reference to an important condition of the theory: the size of the mutational steps involved. Clearly if these were very small, almost continuous evolutionary progress could result. That many genes which become incorporated in the species have, in fact, arisen by mutations which gave rise to minute changes will be apparent from a consideration of the discussion in Chapter III (Section 1), in which it was shown that beneficial mutations will most often involve changes of small magnitude. It is, however, well known that many genes do produce striking effects, and to these the criticism now under discussion might at first sight seem to apply. It is, however, to be noticed that many such genes are successful and have been able to establish themselves in nature: among many other forms, the Lepidoptera, especially those displaying mimetic resemblances, show numerous clear instances of this. In Papilio polytes, Papilio memnon, and the genus Hypolimnas, for example, polymorphism involving the most striking changes is certainly controlled by single genes or super-genes, p. 95. It may then be inquired how adaptations such as these have been brought about.

We would of course agree with Professor MacBride that it is quite unthinkable that mutation after muta-
EVOLUTIONARY PROBLEMS

Evolution could have appeared until at last one happened to hit off the wonderful resemblance which we see between mimic and model in these insects, and that this could have happened repeatedly in a great number of species. As originally pointed out by Fisher (1927), the solution is probably to be found in the interaction of individual genes with the gene-complex, in the manner already outlined.

We have no reason to assume that when genes such as these first appeared their effects were similar to those which they produce to-day. On the contrary, we may suppose that in a given palatable species a gene arose which chanced to give some slight resemblance to a protected form. This would gradually be improved by selection of the gene-complex, and the consequent alteration of the effects produced by all the genes acting together, until an accurate mimicry had been attained. Such a process would be one of slow continuous change, but at the end the profound difference so produced would still be under the control of a single factor; yet this would not mean that the mimic had arisen from the non-mimetic form suddenly by a single act of mutation.

It will thus be apparent that though genetic factors have their origin in spontaneous mutation, this does not in the least imply that the characters which they control are not susceptible of slow and continuous evolutionary change.

This is a conclusion of considerable importance. It is, of course, an extension of the theory of dominance which was discussed in the last chapter, and it is evident that an advantageous gene will become completely dominant, in the manner there described, at the same time that its effects are being improved. There is, of course, no need to assume that such a gene possessed
any advantage from the outset. Initially disadva-
nantageous and virtually non-adaptive genes may ultimately
become established through changes either in the ex-
ternal or the internal environment. A character which
is of no advantage at one period in the development of
a species may be useful at another, and a factor which
is of no value in one gene-complex may have beneficial
effects in another, while the recurrent nature of mutation
allows the genes to make repeated bids for success.
It is evident that domestication, with its artificial
selection, will greatly increase the rate at which genic
improvement can take place. It is to be expected that
when attention is more generally directed to this matter
such changes will be observed in numerous domesticated
species. They had been detected even when this book
first appeared. For example, the fish *Lebistes reticulatus*
had for many years been bred in captivity for aquarium
purposes. The males are polymorphic, and Winge
found that the various forms supplied by dealers are
often more 'beautiful' than those to be obtained in
the wild state, suggesting that appreciable modification
has been brought about by human selection (see Fisher,
1930a, p. 399). Furthermore, Winge (1927, pp. 34–5)
was himself able to show that the effects of one of
these genes, that known as *maculatus*, could definitely
be altered by selection.

Although in natural conditions such processes as these
may often require long periods of time, it seems that
special opportunities for genic improvement sometimes
present themselves. All populations are subject to
marked and often extreme numerical fluctuations which
they generate autonomously, as it were. The environ-
ment is never constant and, when it favours a popula-
tion, some aspects of selection will be relaxed; the
numbers will therefore increase, and genes otherwise
unable to establish themselves will spread. They can then be combined in a variety of new ways, some of which may interact to produce a favourable effect. Such useful combinations will be at a premium when changing conditions later provide a less favourable environment for the organism; the population is then reduced, and the stricter selection which supervenes eliminates those disadvantageous genes and gene-combinations which have been allowed to establish themselves. Thus numerical increase inevitably prepares the way for reduction, and the reverse; so giving rise to fluctuations in numbers, with alternating periods of high and low variability. The new gene combinations rapidly achieved during these cycles would require an immense period of time to produce in a numerically constant population. Selection will favour the establishment of close linkage between those which are of value, in the way described on p. 95, so holding them together.

Considerable attention has in the past been directed to a limited group of special instances in which alternating periods of abundance and rarity coincide over extensive areas. Such cycles are doubtless climatic in origin, and have been associated among other things with the waxing and waning of sun-spots. Yet they have in fact been detected in very few species, a small selection of rodents and animals of value to the fur trade, and they are of negligible importance compared with the automatic fluctuations in numbers to which organisms in general are subject. These, of course, are not necessarily synchronized from one locality or species to another, and their extent and significance is usually much underestimated by those biologists who are not practised ecologists. The isolated population of the butterfly Melitaea (Euphydryas) aurinia studied by H. D. and
E. B. Ford (1930) provided the first instance in which their effects were recorded. This colony was kept under observation for nineteen years in all, and records of its condition had been made by collectors during a previous period of thirty-six years, while preserved specimens obtained at intervals during that time were available for comparison with each other and with those taken subsequently. A fairly accurate study of this particular population was therefore possible for a total period of fifty-five years, and there is one generation annually.

During that time a marked fluctuation in numbers occurred. The colony was well separated from any other in the district, and confined to a very limited area: a few swampy fields from which the imagines seldom strayed even for a hundred yards or so, for they are very localized in habit, and fly but weakly. It therefore formed a well-isolated unit.

In 1881 the species was quite abundant in this locality, and it continued to be so, but with a slight increase, until 1894, by which time it had become excessively common, the butterflies occurring 'in clouds', as the records say, during the few weeks that they are on the wing. After 1897 the numbers began to decline, and from 1906 to 1912 they were quite small. From 1912 to 1920 the insect was extremely rare, only a few specimens being found each year where once they could be seen in thousands. From 1920 to 1924, however, a very rapid increase took place, and from that time until 1935 it remained extremely abundant.

The amount of variation was small during the first period of high density and while the butterflies were becoming scarce. Indeed, a constant form may be said to have existed at that time, and even small departures from it were quite infrequent. When the numbers were rapidly increasing, however, an extraordinary out-
burst of variation occurred. Hardly two specimens were alike, and marked departures from the normal form of the species, both in size, shape and colour, were very common. A high proportion of these were deformed in various ways; the amount of deformity being closely correlated with the degree of variation. When the rapid increase had ceased these undesirable elements practically disappeared, and the population settled down once more to a comparatively uniform type which, however, was recognizably distinct from that which had prevailed during the first period of abundance. Thus an opportunity for rapid evolution had occurred, and evidently the insect had made use of it. It will be noticed how closely the observed changes in abundance and variability followed the course, and produced the results, predicted on general grounds.

It is unfortunate that during the years of observation from 1917 onwards precise numerical estimates of this colony of *M. aurivis* and of the changes which occurred in it, could not be made, as they would now be. But the methods for obtaining them, by means of marking, release and recapture (Fisher and Ford, 1947; Ford, 1953), had not been devised at that time.

The strong probability that the effects of the genes are multiple has already been discussed. This consideration throws some light on the nature of the characters normally used in separating local races and closely allied species. It is a striking fact that these often appear to be non-adaptive or of very small selective importance.

It is evident that certain genes which either initially or ultimately have beneficial effects may at the same time produce characters of a non-adaptive (or disadvantageous) kind, which may therefore be established with them. Such characters often serve most easily to
distinguish different races or species; indeed, they may be the only ones ordinarily available, when the advantages with which they are associated are of a physiological nature. Further, it may happen that the chain of reactions for which a gene is responsible is of advantage, while the end product to which it gives rise, whether in a juvenile or in the adult stage, is of no adaptive significance.

J. S. Huxley (1927) has pointed out another way in which non-adaptive or disadvantageous specific and other differences sometimes arise. For he has shown that changes in absolute body size, controlled by selection, may automatically lead to disproportionate growth in a variety of structures, such as horns and antlers in Mammalia, and the appendages of Arthropoda. The effects so produced may be striking but, as they are the inevitable result of alteration in size, they can rarely have an adaptive significance.

Thus though many of the characters available to taxonomists may be non-adaptive, or actually harmful to the organism, we are not to suppose that they have been established by any process of non-adaptive evolution. In the instance already discussed, that of numerical fluctuation in *Melita aurinia*, the distinction between the old and the new forms was a small difference in colour and marking. In the circumstances, this would appear to be non-adaptive. We may, however, be sure that it was associated with an adaptive change of some more subtle nature. The strong probability that the genes which affect the colour, size and pattern of this insect also control physiological processes in the body, is indicated by the close correlation between all the more extreme variations and deformities of various kinds.
3. Summary

It is important to decide whether or not the whole of organic inheritance is of the Mendelian type. The possible supplementary methods can be grouped under two main headings: that inheritance may in part be purely maternal, and that, in so far as it is bi-sexual, it may to some extent depend upon elements which blend. The evidence indicates that though genes are present in the cytoplasm, by far the largest number of them are situated in the nucleus, and therefore transmitted bi-sexually. In regard to those responsible for the main outline of development characteristic of the phylum, class, or order to which the individual belongs, the evidence is less clear. The facts are, however, consistent with the view that such fundamental characters as these are also controlled by nuclear action. In regard to the second alternative, a more definite statement can be made. The assumption of blending inheritance is not only unwarrantable in face of the experimental evidence available, but it can be excluded even as a possibility, both on account of the mutation rate and because the F2 generation is universally more variable than the F1.

We find that the effects of the genes may be altered by selection operating on the gene-complex. There is thus no reason to assume that when a gene first appeared its effects were similar to those which it produces to-day. The facts of mutation are therefore quite compatible with the slow and continuous course of evolution.

It is further apparent that a gene which has ultimately been selected may not have been beneficial from the outset. The fluctuation in numbers to which species are subject provides special facilities for placing initially non-adaptive or even disadvantageous genes in a number of different gene-complexes, with which they have the
opportunity of reacting in new and possibly beneficial ways. Such fluctuations therefore enable evolution to take place more quickly.

The multiple effects of the genes allow non-adaptive characters to be established in a species through selection of associated advantages. Such characters will often serve most easily to distinguish local races and closely allied species, the differences between which, though in reality adaptive, may appear not to be so.
CHAPTER V
RAPID EVOLUTION IN WILD POPULATIONS

T\he greatest change which has befallen evolutionary theory since this book was first published a third of a century ago is the realization that high selective advantages, up to 40 per cent. and more, are quite usual in wild populations, instead of being very exceptional indeed and rarely exceeding 1 per cent. as previously supposed. Consequently we now know that micro-evolution can take place rapidly, and that it can therefore be studied effectively in wild populations by means of observation and experiment. For that purpose it is, however, necessary to choose instances in which these powerful selective differences are operating. They are due to several distinct conditions of very general application, and it is proposed in this chapter to consider what these are, and briefly to review them.

One of the most important of them has already been discussed on pp. 74-7: that is to say, the great numerical fluctuations automatically generated, to which organisms are subject. This concept, exemplified then as now by means of the butterfly Melitaea cinxia, was woven into the argument of the previous chapter when this book was originally written. Even then it was used to indicate that micro-evolution may take place far more quickly than was generally appreciated. It seems appropriate, therefore, both to the construction of this book and as throwing light on the development of the
subject, to leave it, but little altered, where it was originally introduced, rather than to transfer it to take its place here among those phenomena having similar effects in the sense that they greatly accelerate the evolutionary processes.

The subdivision of a species into small isolated units also favours its rapid evolution. This it does because each group can then fit itself to the special ecology of its own locality, whereas a population occupying a large continuous area can be adjusted only to the average of the conditions which obtain there. Apart from polymorphism (pp. 94–106), such a response is achieved in respect of multifactorial conditions and those controlled by polygenes; that is to say, by large numbers of factors having small additive effects. For these are relatively free from the deleterious changes so generally produced by the 'major' genes which alter the characters and the physiology of the organism considerably.

Thus if a quantitative study be made of any form which is split up into separate groups, it will generally be found that those inhabiting small areas are more dissimilar from each other than those occupying large ones. Fluctuations in numbers tend to increase this effect and, although these must be generated in all communities, their influence upon evolution must be most marked in those of small size.

Some of these considerations are well illustrated by work on the Meadow Brown butterfly, Maniola jurtina (Dowdeswell and Ford, 1933; Dowdeswell, Ford and McWhirter, 1937). In this insect the underside of each hind wing may bear small submarginal spots, which can vary in number from 0 to 5. Their frequency-distribution is generally very different in the two sexes. There is in the male a large single mode at 2 spots in all English, though not in all Irish, localities so far studied. Though
RAPID EVOLUTION IN WILD POPULATIONS 83

it is now known that the frequencies at the rarer values are subject to geographical variation, we are here concerned with the female situation only, in which the spot-numbers provide a sensitive index of evolutionary adjustment. The following account therefore is restricted to that sex. In it, the arrangement may be unimodal at 0 (the condition characteristic of most of southern England and continental Europe) or at 2 spots, while it can also take bimodal and other forms.

The spot-distributions of M. jubata have now been studied in many parts of England, but the results obtained in the Isles of Scilly are especially relevant to the present discussion. The populations have been analysed there on five small islands, of forty acres or less, and on three large ones, of 680 acres or more. Thus the difference in area between the two types of locality is considerable, being at least seventeen times. With two exceptions to be mentioned later (p. 88), the spot-frequencies on every island have remained stable throughout the whole period of study, involving in some instances ten generations; the insect having but one brood in the year. The distribution of spotting was effectively similar on all three large islands during the first six seasons in which collecting was carried out, with approximately equal values at 0, 1 and 2 spots (Fig. 7). However, it differed greatly from one to another on each of the five small islands in the same period, being unimodal at 0 or at 2, or bimodal (Fig. 8).

Various theories can be advanced to account for the similarity of spotting on the large islands and its dissimilarity on the small ones. But it appears that all save one of them can be dismissed. In the first place, it might be suggested that the similarities are due to migration. This is quite impossible. It has been...
established that even a hundred yards of unsuitable country forms an almost complete barrier to this insect (pp. 89-90), while even the two nearest islands on which the spot-distributions are similar are separated by a mile of sea. Moreover, between several of them, other islands on which the spotting is quite different are interposed.

Secondly, this situation has been cited as an example of 'random genetic drift'. That concept is one which has been developed by Sewall Wright in America. He suggests that in small populations the effects of random
RAPID EVOLUTION IN WILD POPULATIONS

Fig. 8.—Spot distributions of female Meadow Brown butterflies on five small islands in the Isles of Scilly.
survival may be important compared with selection. In elaborating this theory he also holds that when selection is relaxed the gene-complex may pass from one adaptive type to another, from which it cannot escape even to obtain a superior advantage when conditions become more rigorous. He likens the process to the passage from one adaptive 'peak' to another across a valley of less perfect genetic adjustment. This geological simile is wholly unrealistic and has done much harm in biology; assuming, as it apparently does, that ecological conditions are so stable that a given type of genetic adaptation, that is to say a given 'peak', is persistent. As my colleague Dr. P. M. Sheppard has remarked, the surface of the heaving sea, in which the peaks of one period become the valleys of another, would be a better simile: that, however, would not at all suit the theory.

Random survival can be important in evolution only if the selective advantages against which it is opposed are small. This it seemed reasonable to assume at the time when genetic drift was favoured; but, as already indicated, it is now known that large selective advantages are in fact common in natural populations. But even apart from that consideration, random drift can be important compared with selection only in small populations. Consequently, the diversity of the M. jardini on the small islands of Scilly and its similarity on the larger ones seemed to provide an example of it. This, however, it cannot do. Random genetic drift cannot be held effective in the presence of even very mild selective forces in populations of much over 500, and those on the small islands of Scilly far exceed this. That on the island of Tean was formerly divided into three, but now into two, and it was quantified by the technique of marking, release and recapture, as exceeding 15,000
RAPID EVOLUTION IN WILD POPULATIONS

individuals in one of them. On St. Helen's it is certainly larger and, though the total on Arthur may hardly exceed 1,000, on the other small islands it is at least as great as on Tean. Consequently, the numbers are not within the scale at which random genetic drift can explain the observed phenomena. Nor is the stability of the populations on the small islands at all in accord with such an interpretation.

Thirdly, it may be suggested that the diversity on the small islands and uniformity on the large ones is due to fluctuation in numbers. Two concepts must here be distinguished. There is the effect of numerical fluctuation operating as a result of decreasing and increasing selective advantages as described in the last chapter. Doubtless this has in the past greatly hastened the micro-evolution of M. jurtina in Scilly, though we have not yet been fortunate enough to witness such an occurrence there. Alternatively, a very different point of view has been put forward: that so great a fluctuation in numbers may formerly have taken place in Scilly that the populations on the small islands were reduced to a few individuals. The chance characteristics of these might then determine those of the colonies to which they later gave rise, while on the large islands the numbers might well have been great enough, even at their minimum, to preserve the original characteristics of the species.

This suggestion also is quite inadequate to cover the facts. In such circumstances, one could imagine a rare gene being lost from a greatly attenuated population. But no type is absent from one small island and present on another: it is only their frequencies which are different. Moreover, if the original minimum constitution in the population is supposed to determine its subsequent history, we return to the difficulties of non-adaptive evolution just discussed under random drift.
However, we have complete evidence that the differences in these small Scilly populations can be produced without any such great reduction in numbers. Female spotting has been changing, from unimodal at 0 to a higher value, on one half of White Island since that habitat has been divided into two by an incursion of the sea in 1961. Furthermore, in one instance, involving one of the populations on the island of Tean, a marked change has occurred in a single generation: from a bimodal type with a somewhat lesser mode at 0 and a greater one at 2 to a completely unimodal distribution at 2 spots (Fig. 9). This was associated with the most striking ecological change which we have witnessed in the islands: the profound effect upon vegetation caused by the removal of a herd of cows. That two such events, unique in our experience, should coincide fortuitously need hardly be considered: the one must have caused the other. But what is relevant here is the fact that this adjustment in spotting did not depend upon
RAPID EVOLUTION IN WILD POPULATIONS

reduction of the colony to a few individuals from which it had later to be recruited.

We return to the proposition from which we started: the one which alone offers a consistent explanation of these phenomena. That is to say, colonies occupying small areas can be adjusted to the special characteristics of their habitats, while those occupying large ones can be adapted only to the average of the conditions obtaining there. Such averages will be relatively similar.

Indeed, we have a test in progress which should demonstrate the truth of this concept by experimental means. However, it should now be clear that the subdivision of a population favours its rapid evolution. How effectively it can do so is illustrated by the immediate response of one of the Tean colonies to changed conditions.

Not only does the subdivision of a population into small isolated groups favour its rapid evolution, but this is achieved far more often and more effectively than had in the past been realized. Some species are migratory, others wandering, but many are extremely localized even when possessed of good powers of dispersal. Thus one hundred yards of unsuitable terrain acts as an almost complete barrier to M. firstina, though it can, and constantly does, travel a greater distance than this in a few minutes in areas suited to it.

The island of Tean, Isles of Scilly, was for years subdivided into five ecological regions; three were hilly tracts of bracken, bramble and long grass, inhabited by the butterfly. One of these was large and central, and it was separated from the two others by promontories of short lawn-like turf from which the butterfly was absent. These were respectively 200 yards and 120 yards in length. The insects could be seen to fly out over them for twenty or thirty yards and then turn and
make their way back, as they do over the sea. Consequently, half-way along these 'lawns' they were absent, though exceedingly common elsewhere. Moreover, specimens were being caught in great numbers and marked with dots of cellulose paint for the purpose of quantitative analysis. They were, in addition, given a mark to indicate from what region they came, and interchanges were found to be very rare (Dowdeswell, Fisher and Ford, 1949).

Similarly, we have long been studying the Scarlet Tiger Moth, Panaxia dominula, in two neighbouring localities in Berkshire (Fisher and Ford, 1947; Sheppard, 1951b). These are isolated marshes of twenty acres or so each, and approximately a mile apart. They are separated from one another by agricultural land. The insect, which is day-flying, is fast and powerful on the wing, often rising to a considerable height. It is sometimes abundant in its localities and, though conspicuous, it has only once been observed outside their confines, and then but a few hundred yards from one of them. The genetic structure of the two populations is quite distinct, indicating that there is no effective interchange between them.

These instances are typical of a situation which is proving far commoner than anticipated; that small ecological barriers act as powerful isolating agents to many species capable of crossing them easily and quickly. The subdivision of natural populations into isolated units is thus more effective than it was thought to be twenty years ago.

One complete and effective type of isolation frequently utilized by plants is rarely available to animals; it is that provided by polyploidy (pp. 23–4). As pointed out by Darlington (1956), autotetraploids have certain
Rapid Evolution in Wild Populations 91

Advantages when a species is extending its range. These are due to irregular meioses, to which they are subject, giving rise to new types of variation. It should also be noticed that as a result of their larger nuclei, and therefore larger cells, such plants are giants whose size may be useful in certain kinds of competition. These forms are completely isolated from normal diploids, for crosses with them produce triploids which are sterile.

The tetraploids themselves are of reduced fertility, owing to the abnormalities in chromosome-pairing to which they are subject. This is fatal to them from the point of view of long-term evolution, but it may be no handicap in rapid adjustment to new conditions and for two reasons. Firstly, plants are generally much more fertile than is needed for their normal propagation. Secondly, the autotetraploids may be able to reproduce vegetatively. Ability to do this, like all other characters, is subject to genetic variability, and selection will favour those tetraploid individuals in which such reproduction can take place easily. Indeed, as Darlington points out, wild autopolyploids of all types so constantly show unusual capacity in this respect that, had not experiment demonstrated otherwise, it might be thought that increased vegetative propagation is itself an outcome of multiplying the chromosome-sets.

Thus there is no barrier to the short-term exploitation even of the sterile triploids which arise not uncommonly in all plants. They too have their advantages, for they benefit in vigour: partly because they are relieved from the heavy drain of pollen or seed production.

It is often found therefore that the plants spreading into fresh habitats are polyploids. This is true whether we consider extensions beyond the normal range of the species or the colonization of areas within it which have but recently become available owing to a change in land...
usage, such as the cutting down or the planting of woods.

Few animals are capable of self-fertilization or of reproducing asexually. Consequently the road to rapid short-term evolution by means of polyploidy, as a result of the special advantages and of the isolation which it confers, is generally closed to them.

It is for this reason that animals respond somewhat differently from plants to the conditions found at the edge of their range. These they generally meet by con­fining themselves to some specialized set of conditions which chance to be favourable, and adjusting themselves accurately to them. Thus on the extremity of their distribution animals are often wholly restricted to environments to which they are not at all confined elsewhere.

In addition to promoting genetic isolation, allopolyploidy (p. 24) can give rise to very rapid evolution in wild populations owing to the way in which it creates new species. Of this, the rice-grass Spartina provides a notable illustration. Spartina stricta is native to Britain; its diploid chromosome number is 56, though it is really an adjusted octoploid from the basic number of the group (7). It appears that chromosome doubling occurred in a hybrid between this and S. alterniflora, which was imported from America. The latter, really a decaploid, has an effective diploid number of 70. The allotetraploid so produced therefore possesses 126 chromosones. It is fertile, though sterile with both the parental forms, and constitutes a new species known as S. townsendii. This first appeared in Southampton Water about 1870 and has since spread to other stations along the south coast of England, notably Poole Harbour, where it has multiplied greatly and is becoming a pest (Huskins, 1900). It must have been at an advantage
RAPID EVOLUTION IN WILD POPULATIONS

compared with its imported parent whose opportunities for gaining a foothold would initially have been at least as favourable, since it was in a position to form a natural hybrid. For more remarkable, however, is the fact that it has even proved superior to the native species. That this hybrid should actually compete successfully with both its parental forms indicates that the interaction of their two gene-complexes must have given rise to some new and superior quality. We have here an outstanding instance of the importance of genetic variability of this kind, and of the sudden and successful establishment of a new species in the countryside.

Darlington gives other examples in his masterly discussion on chromosome adjustments in plants (1956). Many of the mechanisms involved are of fundamental importance in evolution. Here in this chapter, however, we are concerned with those evolutionary changes in wild populations which take place so swiftly that they can be subjected to direct observation and experiment. In addition to allotriploidy, these, as he points out, may be provided by an autotriploidy reaching the chromosome number of some other allied species with which it can then cross and produce a host of new forms. Valeriana officinalis affords an instance of this kind. Diploids, with 14 chromosomes, are found in Europe. But the colonizing plants at the edge of their range are tetraploids and these alone have reached England, where they inhabit dry and alkaline soils. Here and there they have given rise to octoploids, which have the same chromosome number as V. sambucifolia (56) with which they can accordingly cross. From the great range of resulting hybrids, forms have been selected capable of growing even in wet and acid situations.

It has for a considerable time been realized that large
selective forces must be involved in polymorphism. This condition is defined as the occurrence together in the same habitat of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation (Ford, 1940b, 1945). That is to say, distinct phases are maintained in the population by a switch mechanism which, in fact, is almost always genetic. The condition is extremely effective in promoting the rapid evolution of characters controlled by single genes because both members of the allelomorphs, or sets of super-genes (p. 95), concerned are quite common in the population instead of one being very rare, as in other situations involving major genes contrasted with the multifactorial and polygenic conditions. Polymorphism is subdivided into the Balanced and Transient types (Ford, l.c.).

In balanced polymorphism, two or more alternative forms are maintained by a balance of selective advantages. The most general way in which this can evolve is for the heterozygote to be favoured compared with either of the other genotypes. It seems that this situation will automatically arise when a major gene, previously eliminated by selection and maintained merely by recurrent mutation, acquires an advantage owing to a change in the environment: whether directly or through some resultant adjustment in the gene-complex. Since mutations are generally deleterious (pp. 43-6), if one of the effects of a gene becomes beneficial the others will almost certainly be harmful. The advantageous character will then become dominant and the disadvantageous ones recessive, and this will occur with exceptional speed owing to the high frequency of the gene concerned. In such circumstances, the heterozygote will have only good qualities, while both homozygotes will have some good and some bad. Thus the hetero-
zygotes must gain an advantage and polymorphism will ensue.

It is for this reason that even when the ecological situation is itself such as to maintain polymorphism, evidence is accumulating to show that the heterozygotes are still the more favoured genotype: a 'double assurance' of polymorphism, as it were. An example is provided by Batesian mimicry, studied especially in insects but known in other groups. Here a palatable form copies one which is protected: by poisonous qualities, a nauseous taste, or a sting. As the numbers of the mimic rise compared with the model, so the advantage wanes. It is converted to a disadvantage when it reaches the level at which a given pattern is associated more decisively with edible than with inedible qualities. It is therefore usual for Batesian mimics to copy several models, their phases then being maintained in balanced polymorphism at such frequencies that each receives equal protection. A number of mimetic butterflies have now been studied genetically; and in several of them (Papilio dardanus, *P. polytes*, Danaus chrysippus) the heterozygotes exceed expectation in segregating families.

Genes may interact with one another to produce an advantageous effect, and this is especially likely to occur when they are involved in the control of the same physiological processes. When they do so, selection will tend to produce close linkage between them, so that they can together form a unit or 'super-gene' to act as a switch in determining alternative forms. Thus, when on different chromosomes, a translocation bringing them on to the same one will be favoured, so too will anything which then reduces crossing-over between them, whether by means of inversions or a reduction in chiasma frequency in the region concerned (pp. 25-6). Thus balanced polymorphism is often associated with close linkage.
(Fisher, 1930a; Sheppard, 1953), which when first discovered has sometimes been mistaken for allelomorphism.

In view of these considerations, it is not surprising that polymorphism is proving to be far more frequent than was supposed when the first edition of this book appeared. As with other mechanisms already quoted as involving large selective advantages in natural populations, instances of it can be used in the experimental study of evolution. A few of these may briefly be mentioned.

The snail *Cepaea nemoralis* is polymorphic both for colour and banding. Yellow shells are recessive to the brownish shades (brown, reddish, pink) and the possession of bands is recessive to their absence. There is linkage between the genes concerned. The particular colour of the darker shells and the number of the bands is also controlled genetically. The one-banded condition (up to five are possible) is certainly unifactorial. The genetics of the other banding numbers, and of the subdivisions of the darker shades, has not yet been fully analysed.

The yellow shells are the less conspicuous upon light soils such as those of a chalk down, and upon green herbage, while the brownish are the better concealed in a beech wood, or upon dead vegetation in general. The snails are preyed upon by thrushes, which carry them to favourite stones (thrush anvils) where they break them open. Cain and Sheppard (1950) found that brownish shells are much the rarer among the *C. nemoralis* populations on chalk downs and much the more common in beech woods. They discovered, however, that those destroyed by thrushes include an unduly high proportion of the inappropriately coloured forms. Sheppard (1951a) also used this species to conduct a penetrating analysis of evolution in progress. He studied the
RAPID EVOLUTION IN WILD POPULATIONS 97

proportions of the two main colour types in a mixed deciduous wood, and of those destroyed there by thrushes, from mid-April to mid-May. During this period the background passed gradually from brown to green, and as it did so the proportion of brownish shells taken by the thrushes increased: the yellows having at first been the more heavily eliminated were at the end of the period less so. Sheppard showed that this was not due to a detectable change in the proportions of the two types in the locality. He also demonstrated that the thrushes were not bringing the snails from a different feeding ground. This he did by marking large quantities of the shells with a dot of cellulose paint, but underneath so that their appearance was not affected.

Similarly, the banded shells can be shown to have an advantage on a diversified background, such as a mixed hedgerow, and the plain upon a uniform one. The linkage between the genes for colour and banding allows a genetic constitution to be built up in which the combined type favoured in a locality is that generally produced.

It is important to notice that though the inappropriate types of colour and banding are constantly being eliminated in each locality, the populations do not become uniform. We have here a clear indication that the respective heterozygotes are at a physiological advantage compared with the homozygous types.

No wild populations of any animal have been analysed so fully as those of Panaxia dominula in two localities, Cothill and Sheepsted, near Oxford (p. 90). The insect has one generation a year and at Cothill it has been studied from 1938 onwards. It is polymorphic there owing to the occurrence of a variety medionigra, which is almost unknown elsewhere. This is a heterozygote, with a gene-frequency of about 1.5 to 11.1 per cent., according to the season. It is subject to
considerable variability but resembles more closely the normal than the mutant homozygote. It is characterized by an extra black spot on the red hind wings and the reduction or absence of the central cream-coloured one on the bronze-green forewings.

The size of the population and the frequency of the *medionigra* gene has been estimated each year by the method of marking, release and recapture. Now under Mendelian inheritance it is possible to calculate whether changes in gene-frequency are or are not too large to be fortuitous, provided the total size of the population be known. Here the data for such a deduction are all available, and they prove that the seasonal variation in the percentage of *medionigra* is too great to be due to random drift: that is to say, it must be determined by selection. This was the first instance in which such a comparison could be made (Fisher and Ford, 1947; Sheppard, 1951b).

We do not yet know upon which characters produced by the *medionigra* gene selection operates most strongly, but they are probably of a physiological nature: a conclusion to be reached on general grounds (pp. 34-41). It is at least supported by the observation that the rare homozygote, known as *bimacula*, is noticeably lethargic. In that genotype, the disruptive colour-pattern of the forewings is obliterated by black pigment; for only two of the pale (white or yellowish) spots remain, and these the two basal ones. In consequence, we find it decidedly conspicuous. However, the heterozygote is hardly affected in this way, but Sheppard (1952) has discovered that the gene influences the mating-habits of the insect. The males are unaffected, but the females show a significantly high tendency to mate with any other of the genotypes rather than their own. This extraordinary situation represents one of the few instances in which
The genetic control of habit has been detected. As Sheppard points out, it would itself lead to a polymorphism, and in the following way. The two sexes are present in approximate equality. Each male can pair a number of times but the females, to which they are attracted by scent, can do so once only. There is thus mating competition among the males, which crowd to the virgin females, and those of the rarer genotype will be favoured. We now know that forces opposed to this tendency are also at work, for it has been established that medionigra has a low male fertility while its survival rate from egg to imago is about 75 per cent, that of dominula.

By selection experiments of the kind already outlined (pp. 55, 60), it has been possible in four generations to establish lines in which the heterozygous expression of the medionigra gene was, on the one hand, increased and, on the other, decreased: that is to say, the dominance of the gene had been modified in either direction. A similar, but much slower trend has been recognized in nature, the characteristics of medionigra having gradually become more distinct. It is true that, as so often in the heterozygote, the expression of this gene can be modified by the external environment: in this instance by temperature. But, especially in England, it appears vain to interpret such a consistent trend in terms of climatic changes. It is presumably due to a selective modification of the effects of the medionigra gene, one which has been fostered in the laboratory. Finally, it will be noticed that this analysis of evolution was possible only because the species selected for study was one in which large selective differences were operating in a wild population.

Genetic variability must be due to genes which are either harmful, neutral or beneficial in their influence.
upon the organism. If harmful, they can survive only at an extremely low frequency, being eliminated by selection and maintained merely by recurrent mutation. Fisher (1930c) has shown that for the members of a pair of allomorphs to be of effectively equal survival value, the balance of selective advantages to which they are exposed must be extraordinarily exact. Consequently this situation must be very rare. Moreover, a mutant gene, when selectively neutral, can spread through the population only at an exceedingly slow rate. It can therefore have made but little progress before the accurate balance required for neutrality is upset by changing conditions. Thus if a character unifactorily controlled occurs even in as much as 1 per cent. of the population, it must be favoured by selection and constitute a polymorphism with all the consequences which flow from that situation. They are such that important deductions can be made from them, as may be illustrated from the human blood groups.

These were first treated as balanced polymorphisms in 1942 by Ford, who had already shown in 1940 that they must be of unequal survival value. This was before the discovery of Levine, Katz, and Burnham (1941) that the Rhesus groups can produce haemolytic disease of the newly born, and that this arises from a serological incompatibility between mother and foetus. It is surprising, therefore, that it has been maintained until recently, both by anthropologists (e.g. Boyd, 1940) and geneticists (e.g. Dobzhansky, 1951, p. 156), that the blood groups may be non-adaptive. In fact, the contrary follows as an inevitable consequence of their genetic switch-control, combined with the occurrence of the rarer types in several per cent., often in a considerable proportion, of the population in some, and generally in many, human races. Thus it was reasonable to conclude.
RAPID EVOLUTION IN WILD POPULATIONS

that those possessing certain blood groups would prove more susceptible than others to particular diseases, a prediction made by Ford in 1945. The first definite verification of it appears to have been provided by Aird et al. (1952), who showed that a significantly high proportion of those suffering from cancer of the stomach belong to the group A of the ABO Series. Indeed, the previous work of Struthers (1951) had strongly suggested that a greater proportion of group A than of group O babies die of broncho-pneumonia during the first two years of life, though the results were not fully significant. Further evidence of the association between blood groups and disease is now rapidly accumulating. The situation in regard to duodenal ulcer has been subjected to an especially complete analysis by Clarke et al. (1955, 1956), who have shown that group O individuals of this same Series are 35 per cent. more likely to develop it than are others.

Duodenal ulcer patients also undoubtedly include an undue proportion of non-secretors of the ABO antigens, a comparison which holds good not only in the ordinary controls but for the normal brothers and sisters of such cases (Clarke et al., 1956). It may be remarked that another polymorphism, controlled by a simple genetic switch-mechanism, is here involved; for while the majority of the English population secrete these substances freely into the saliva, a dominant characteristic, approximately 22 per cent., representing the recessives, do not. Indeed, various other human polymorphisms involving physiological qualities are known or are now being analysed. One of them which has long been recognized is the ability to taste a sulphur compound, phenyl-thio-urea. This is a simple dominant, a class which includes about three people out of four in north-western Europe. These, the "tasters", are significantly more liable to toxic diffuse goitre than are the
We have so far been discussing balanced polymorphism. The transient type (p. 94) is that in which a gene previously eliminated by selection acquires some advantage owing to changes in the environment and, therefore, spreads through the population. While it does so, the characters controlled by the two alleles concerned become polymorphic. That condition may continue until what was once the normal form is reduced to the status of a rarity maintained only by recurrent mutation. Alternatively, before that limit is reached, continuing selective advantages may establish an equilibrium so that the transient type passes into the balanced one.

The spread of a previously disadvantageous major gene will not often be witnessed, for evolutionary changes are achieved most easily in respect of multifactorial or polygenic conditions, or by adjusting the phases of an already balanced polymorphism. Moreover, the process, when it does take place, may be rather rapid. However, it is exemplified by the spread of black forms among the moths inhabiting manufacturing districts, a phenomenon known as 'Industrial Melanism'. This is the most striking instance of evolution ever actually witnessed in any living organism, animal or plant. It has been reported from several countries, but so far it has been studied intensively only in Britain, where about ninety species are affected. All of these rest exposed upon tree trunks, boughs or walls, deriving protection from a cryptic resemblance to bark or lichen. The first black specimen (var. carbonaria) of the Peppered Moth, *Biston betularia*, was recorded from Manchester in 1850. Over 95 per cent. of the population is now of that form.
RAPID EVOLUTION IN WILD POPULATIONS

there, and it has reached frequencies as high in other industrial areas, while in all of them where it has been studied it has become very common. Kettlewell (1958) has shown that it has also invaded rural districts eastwards of the manufacturing towns, owing to the smoke-drift due to the prevailing westerly winds in this country. The history of the other species is similar, but all stages in the process can be found among them to-day. Most of the melanic forms involved are completely black. The earliest carbonaria were marked with faint pale lines now lost, thus the form has evolved as well as spread.

Various theories have been put forward to account for these extraordinary events, but it is now unnecessary to consider any but the one which has proved correct. It was suggested that two contending influences are involved: affecting respectively the viability of the insects and the efficiency of their protection from predators. A number of breeders had reported that certain of the successful black varieties seemed hardier than the normal forms. This was demonstrated experimentally in the Mottled Beauty, Clossa repandata, by subjecting segregating broods to intense selection through starvation (Ford, 1946b). The resulting ratios departed significantly from expectation in favour of the black varieties. It is likely that the extent of their physiological differences may vary greatly from one species to another, being in some relatively easy and in others relatively difficult to detect; but in industrial melanism they should always operate in favour of the black forms which, in spite of that advantage, have spread only in recent times.

That they have not done so previously is due to the other aspect of the situation: the obliteration in the melanic individuals of the protective colour-pattern upon which their safety depends. The rigour of the
selective forces here operating had been altogether under-estimated, even by those who appreciated their existence: and by many they were denied. No group of organisms has been more extensively collected than butterflies and moths, nor more assiduously observed than birds and, in one respect at least, the majority of entomologists and ornithologists were agreed: that birds do not selectively eliminate resting moths. The remarkable work of Kettlewell (1955) has proved them wholly incorrect. He has shown indeed that such elimination is extremely effective and why it has not previously been discovered. It appears that a resting moth is seized so rapidly, in a flash as it were, that the act can be detected only by means of carefully planned observation on a large scale. Probably many species of birds are involved; Kettlewell has shown that these include Redstart (Phoenicurus phoenicurus), Hedge Sparrow (Accipiter modulius), Yellow Hammer (Emberiza citrinella), Spotted Fly-Catcher (Muscicapa grisola), Robin (Erithacus rubecula), and Nuthatch (Sitta coccia). Working with the Peppered Moth (Biston betularia), he released many hundreds of the normal form and of the black carbonaria, especially bred for the purpose. These were marked with a dot of cellulose paint placed underneath so as not to alter the appearance of the insect, consequently the fate of each individual could be followed. He found that to the human eye the normal form is beautifully concealed on the light lichen-covered trees of rural Dorset, whereas carbonaria is conspicuous, and he showed that the latter is the more subject to elimination by these predators (Kettlewell, 1956). The reverse situation proved to be true in a wood in the Birmingham neighbourhood where lichen cannot grow owing to air-pollution and the trees are darkened by soot. Here the black moths, which to the human eye
RAPID EVOLUTION IN WILD POPULATIONS

Look much the less evident in such conditions, derive the greater protection from birds. The difference, opposite in tendency in the two localities, was heavily significant and indicated that high selective advantages are involved. The numbers released and recaptured in the two districts are given in Table I. These results show that the

<table>
<thead>
<tr>
<th></th>
<th>Liberated</th>
<th>Recaptured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dorset</td>
<td></td>
<td></td>
</tr>
<tr>
<td>typical</td>
<td>450</td>
<td>62</td>
</tr>
<tr>
<td>black</td>
<td>473</td>
<td>39</td>
</tr>
<tr>
<td>Total</td>
<td>969</td>
<td>102</td>
</tr>
<tr>
<td>Birmingham</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Liberated</td>
<td>137</td>
<td>18</td>
</tr>
<tr>
<td>Recaptured</td>
<td>447</td>
<td>123</td>
</tr>
<tr>
<td>Total</td>
<td>584</td>
<td>141</td>
</tr>
</tbody>
</table>

The numbers of normally coloured and of black Peppered Moths, *Biston betularia*, released and recaptured in rural Dorset and in the Birmingham neighbourhood.

The proportion of blacks recovered is, on the assumption that the two types survive equally well, 17.7 per cent. below expectation in the Dorset locality and 10.6 per cent. above expectation in that near Birmingham.

The principles involved in the phenomena of industrial melanism have thus been analysed, though an immense amount of work remains to be done in elaborating them and applying them to other species. Kettlewell finds also that the spread of the black forms may be a more sensitive indication of air pollution, with its potential medical and other effects, than any direct means of measurement so far available (Kettlewell, 1958).

One further point remains. It seems most probable that as industrial melanism reaches a high frequency in a population, the polymorphism involved will pass from
the transient to the balanced type. As already explained, when a character unifactorially controlled begins to spread, it will normally give rise to a balanced polymorphism. The gene will only sweep through the population as a transient polymorphism when the new conditions which favour it have changed so materially from the old, and when it chances to produce effects so well suited to them, that the replacement of the former normal allelomorph by the former mutant one takes place very rapidly. In these circumstances, there may not be time for the development of dominance-adjustment to favour the heterozygote, so giving rise to a balance of advantages and disadvantages.

This is the situation encountered in the highly peculiar conditions of industrial melanism. Here a cataclysm has occurred in the countryside, while many species of moths are, as it were, 'pre-adapted' to meet it by holding in reserve rare mutants physiologically favourable and already suited in appearance to the new, but not to the old, environment. When the pale, and always recessive, form has become a rare variety amounting, say, to between 5 and 1 per cent., the speed of the progress will be much reduced. Yet at this level the heterozygotes, in which the 'wild type' allelomorph is sheltered, still comprise 34·7 to 18 per cent. of the total population. The time and opportunities for their improvement at this stage are therefore considerable, and immediately this sets in, so that they acquire an advantage over the other two genotypes, the conversion of a population to a monomorphic black form is impossible. It is likely therefore that the pale phase will become rare but will not disappear, in the sense of being reduced to the level at which it is maintained merely by mutation.

The study of ecological and geographical races, and
especially of plants and animals at the edge of their range, throws a flood of light upon recent evolution when the type of chromosome analysis described and developed by Darlington (1956) has been applied to them. However, the processes discussed in this chapter, and in the latter part of the previous one, are certainly those which most frequently result in evolution of such a rapid type that it can be subjected to observation and experiment. The instances in which this has so far been done are few, yet they have already produced results so rewarding that we may expect a great advance in knowledge from an extension of work upon these lines.
LIST OF REFERENCES


110 MENDELISM AND EVOLUTION


REFERENCES

- (1940) 'Polymorphism and Taxonomy' in The New Systematics (pp. 493-313), Oxford.
112 MENDELM AND EVOLUTION


Huxley, C. L.: (1924) 'The Origin of Spartina Townsendii', Genetica, 12, 531-3.


Muller, H. J., and Moore-Smith, L. M.: (1930) 'Evidence that
REFERENCES

Natural Radioactivity is inadequate to explain the Frequency of Natural Mutations', Proc. Nat. Acad. Sci., 16, 277-85.


Oliven, C. P.: (1909) 'The Effect of Varying the Duration of X-ray Treatment upon the Frequency of Mutation', Science, 71, 44-6.


Russell, E. S.: (1930)'The Interpretation of Development and Heredity', Oxford.

Schulte, W.: (1930) 'Kältebewirzung eines Städtelernes und ihre allgemeinbiologischen Hinweise', Arch. f. Ent. mech., 47, 43-76.

Shephard, F. M.: (1931a) 'Fluctuations in the Selective Value of Certain Phenotypes in the Polymorphic Land snail Ceruena nemorata (L.)', Heredity, 5, 125-34.

--- (1931b) 'A Quantitative Study of Two Populations of the Moth Parnassius dominula (L.)', Heredity, 6, 343-76.

--- (1932) 'A Note on Non-random Mating in the Moth Parnassius dominula (L.)', Heredity, 6, 230-41.


Sturtevant, A. H.: (1921) 'The Effects of X-rays in producing Somatic

--- (1922) 'Genetic Studies on Drosophila simulans', Genetics, 6, 43-54.

--- (1929) 'Genetic Studies on Drosophila simulans', Genetics, 6, 43-54.


--- (1927a) 'Studies on the Phenotypic Manifestation of Hereditary Factors', Genetics, 15, 125-7.

--- (1927b) 'Studies on the Phenotypic Manifestation of Hereditary Factors', Genetics, 15, 125-7.

--- (1929) 'The Effects of X-rays in producing Somatic
Genovariations of a Definite Locus in different directions in

WENZL, H.: (1928) 'Two new Mutant Characters on the
Spermathecae of the females of *Drosophila melanogaster*",
*Genetics*, 13, 399-409.

WING, O.: (1927) 'The Location of eighteen Genes in *Lebistes
reticulatus*, J. Gen., 18, 1-43.


GLOSSARY

Agouti. The brownish colour produced by hairs which are banded alternately with yellow and black pigments.

Allelomorphs. Genes occupying identical loci in homologous chromosomes.

Autosome. Any chromosome other than a sex-chromosome.

Back-cross. A mating between a heterozygote and a homozygote.

Batesian Mimicry. The resemblance of a palatable to a distasteful species for protective purposes.

Blastula. The stage when the embryo is a hollow sphere of cells with no opening.

Chromatid. The two bodies produced by the longitudinal splitting of the chromosomes preparatory to nuclear division. They become the daughter chromosomes of the two resulting cells.

Chromosome. A deeply staining constituent of the nucleus. The chromosomes take up this substance when dividing.

Chromosomes. One of the deeply staining paired structures which appear in the nucleus during its division. They are present in a constant number in each species and carry the genes.

Cistron. A group of genetic units all controlling the same set of characters and constituting a gene. The mutation of one or another of them is often responsible for producing multiple allelomorphs.

Cleavage. The segmentation of the egg by which the cells of the embryo are formed.

Correlation. The study of simultaneous variation.

Coupling. The association together in linkage of the two dominant or the two recessive characters produced by different pairs of factors (compare Repulsion).

Crossing-over. An interchange of corresponding blocks of material, and therefore of genes between two of the four chromatids, being those derived from different but homologous chromosomes.

Cytology. The study of cell structure.
Cytoplasm. The living substance of the cell, excluding the nucleus.

Diploid cells. Those having the two members of each chromosome pair.

Dominant. A gene which obscures the action of its allelomorph (the recessive) when present with it in the heterozygous state.

Ecology. The relation of living organisms to their environment.

Environmental variation. Variation produced by changes in the environment (compare genetic variation).

F1. The first filial generation; the offspring of a given mating.

F2. The second filial generation; the grandchildren of a given mating, obtained by interbreeding the F1 generation.

Gametes. Reproductive cells of either sex. In higher animals these are the spermatozoa and ova, while in higher plants they are enclosed in the pollen grains and ovules respectively.

Gastrula. A stage in the development of multi-cellular animals when the embryo consists of a two-layered sac.

Gastrulation. The formation of the gastrula.

Gene. An hereditary unit which controls the appearance of definite characters. The genes are paired and are usually carried in the paired chromosomes, where they are situated at distinct loci (see also Cistron).

Gene-complex. The interacting system produced by the whole of the genetic factors of an organism. These combine to make an internal environment in which any given factor must operate.

Gene mutation. A change in a genetic factor.

Genetics. The study of variation and heredity.

Genetic factor. See "Gene".

Genetic variation. Variation produced by changes (recombinations or mutations) in the genes.

Genotype. An organism judged by its genetic constitution (compare Phenotype).

Haploid cells. Those with one member only of each type of chromosome, as the reproductive cells of a diploid.

Heterogametic sex. That with dissimilar sex-chromosomes.

Heteroploids. Individuals which contain a chromosome too few or too many.

Heterozygote. An individual in which the members of a given pair of genes are dissimilar.

Homogametic sex. That with similar sex-chromosomes.
Homologous chromosomes. The members of the same chromosome.

Homogygote. An individual in which the members of a given pair of genes are of similar nature.

Inversion. A section of a chromosome which has broken and reattached itself in its former position but the wrong way round.

Leptotene stage. An early stage in the prophase of the first meiosis in which the chromosomes appear as long thin threads.

Locus. The position occupied by a gene on a chromosome.

Maturation. The period during which the development of the gametes is completed. It includes meiosis.

Mesenchyme. Part of the middle layer of higher animals, which arises in the embryo in the form of wandering cells.

Modifying factors. These modify the characters produced by other genes. They may be without effect by themselves.

Multiple allotomorphs. Genes produced by a number of mutations of different nature at the same locus (see Cistron).

Multiple factors. Genes which have a similar effect, and reinforce each other.

Mutation. The inception of a heritable variation.

Nucleus. A specialized part of the protoplasm within all typical cells. It is essential for the life of the cell and is accurately halved when division occurs.

Parthenogenesis. The development of an egg without fertilization.

Phenotype. An organism judged by its appearance (compare Genotype).

Plastid. Bodies in the cytoplasm of plants, which multiply and are distributed irregularly at cell division.

Polymorphism. The occurrence of several discontinuous forms
of a species together in a common environment in such proportions that the rarest cannot be maintained merely by mutation.

Polyplody. A condition in which more than two members of the chromosome-pairs are present in an organism.

Prophase. The stage preparatory to cell division, when at the first meiosis, the chromosome-pairs conjugate with each other and the chromatids resulting from them interchange material.

Polyploidy. The living substance of an organism.

Pure-line. The descendants of a single self-fertilized individual homozygous for all its factors.

Recessive. A gene whose action is obscured by its allelomorph (the dominant) when present with it in the heterozygous state.

Repetition. The association together in linkage of the dominant character produced by one factor-pair and the recessive produced by another (compare Coupling).

F1 generation. The offspring of a 'back-cross'.

Segregation. The recovery of the original types in definite proportions in subsequent generations, when individuals exhibiting contrasted characters have been crossed.

Sex-chromosomes. The X and Y chromosomes.

Sex-controlled inheritance. Characters which can only be manifested in one or the other sex. The genes producing them may be carried either in the sex-chromosomes or in the autosomes of both sexes.

Sex-linked factors. Those carried in the sex-chromosomes.

Somatic mutation. Mutation taking place in the body cells instead of in those which form the gametes.

Spermatheca. An organ present in certain female animals, in which the sperm received from the male is stored.

Super-gene. A group of two or more major genes responsible for different sets of characters but so closely linked that they can act as a single switch in controlling alternative forms.

X-chromosome. The chromosome carrying the factors which control sex determination.

Y-chromosome. The partner of the X-chromosome in one of the two sexes. It contains but few genes and, in general, does not control sex determination.

Zygote. The first cell of a new individual, produced by the fusion of the gametes. In higher animals and plants it is the fertilized ovum and ovule respectively.
INDEX

Abundance and variability, 74-80
Abunda.nce and variability, 74-80
Aird, 101
Allelomorphs, 3, 18
multiple, 3, 54, 56
Allopolyploids, 24, 92-3
Allopolyploids, 24, 92-3
Amphihion, 14
Anaden, 65
Autopolyploids, 24, 90-3
Alleloincs, 14, 15
Back-cross, 6, 10, 12, 13
Barley, 31-2
Barriers, 82, 84, 86-90
Bateson, 54
Bateson, 54
Blood groups, 100-2
ABO series, 101-2
non-secretors, 101
Rh factors, 100
Bovis, 65, 67
Bovis, 65, 67
Bridges, 32, 54
Bromela-paucoinula, 191
Cain, 96
Cancer, 101

Austin, 55
Castle, 94
Copernicus, 94-7
Chiasma, 18, 55
Chromosomes, 16, 17
Chromosomes, 2, 3, 74
aberranilities in, 21, 23, 24
homozygous, 3
escape of, 14, 19
Cider, 65
Cocker, 34-5, 38
Clarke, 101
Collins, 31, 65
Correlation, 64
Corren, 64
Cotton, 52
Dobzhansky, H.J., 35, 37, 47, 99
Dobzhansky, H.J., 100
Contact, vii
Cytology, 2, 19
Cytolonic inheritance, 64-7, 79
Cytolonic-nuclear relations, 66

Darlington, 98, 99, 107
Darwin, vii
Deletion, 23
Dementia, 58
Diabetes mellitus, 101
Disproportionate growth, 78
Diver, 66
Dobzhansky, 19, 33, 37, 47, 53, 100
129 MENDELM AND EVOLUTION

Dominance, 4
Dominance, evolution of, 44-
52, 73, 94, 99
Dowdeswell, 82, 99
Drosophila, 16, 17, 37, 44, 54
D. funebris, 28, 57
D. melanogaster, 21, 47-8
abnormal abdomen, 31
Bar-eye, 52
black body, 13
hobbled, 56
chromosomes, 12
cream, 2, 35-6
curled wings, 19-20
curved wings, 13
ebony, 53
eosin-eye, 35-6
extra spermatheca, 36
eyes, 39-41
pink eye, 19-20
reduplication, 31
sooty, 53
spermatheca, 37, 53
Stubble, 53
testa-sheath, 37
white eye, 23-16, 22, 27, 47
D. obscura, 47
D. pseudo-obscura, 47
D. simulans, 47
D. virilis, 57
Dobzhansky, 47
Dundee ulcer, 161
Duplicat.ion, 23
Echinocida, 65-7
F 1 and 2, 4, 60, 79
Factor interaction, 34-42
Feldman, 54
Fish, 14, 74
Fisher, vii, 40-7, 52, 55, 57, 60,
68-70, 73, 90, 96, 98, 100
Fluctuation in Numbers, 74-
82, 87
Ford, E. B., 23, 29, 30, 50,
55-6, 76, 82, 90, 94, 99, 103
Ford, H. D., 75
Poultry, see Poultry
Fryer, 56
Gallus domesticus, 55
chromosomes, 12
dwarfing, 30
inter-factorial pigment, 7-11
modifying factors, 50
red eyes, 4-11, 28-50, 49, 50
Gene-complex, 39-41, 45-53,
55-7, 69, 65, 70, 73-4,
79, 88, 94-5
Gee, 3
linear order, 18-19, 23
multiple effects, 37-8, 77
mutation of, 3, 21-4
Genetic drift, 84, 86-7, 93
Genetic factors, 3
Genetic variation, 29, 30
Genetics, vii
Genotype, 28
Gershenson, 47
Godlewki, 65-7
Goldfish, 58
Great Camilly, 88
Growth, relative, 78
Haldane, 55, 57
Haldane, 55, 57
Harland, 52
Hersch, 52
Heterogametic sex, 14, 16-17
Heteroploids, 23
Heterozygote, 3
advantage of, 94-5, 99, 106
Hogg, 51
Homozygous sex, 14-17
Homzygotes, 3, 4
INDEX

Huxley, 29, 50, 78
Hybrid sterility, 24
Independent assortment, 2, 7-11, 25
Industrial melanism, 102-5
Inversion, 85
Johannsen, 69
J. Kettlewell, viii, 103-5
J. Lederer, 74
Lepidoptera, 14, 72, 95
Lepisosteus reticulatus, 74
Leptotene stage, 14
Linneman, 66
Linnge, 12-14, 15, 25, 78, 90-7
Linkage-group, 14
Locus, 18
Lycopersicon, 66
MacBride, 71-2
Man, chromosomes, 12
Muscular tagging, 82-90
Maternal inheritance, 63-7, 79
Maturation, 4, 6, 8, 10, 13, 15
McConnell, 101
M. McClintock, viii, 82
Meadow Brown, see Maniola
Mendel, 1-2, 7
M. M. Morgan, 2, 31, 54, 66
Mott-Smith, 72
Muller, 19, 22
Multiple factors, 25, 82, 94, 102
Mutations, 2, 21-2, 58, 69-73
Nitrogen fixation, 2, 23-4, 80
Nuclear genes, 22, 47, 61, 60-1
Olive, 22
Oliver, 22
P. Painter, 19
Peppered Moth, see Diston betularia
Plastic inheritance, 28
Migration, 83-4
Mimicry, 85
M. J. D. Muller, 64
M. J. S. McWhirt('r, viii, 82
Modifying factors, 26-8, 49-50
Morgan, 2, 31, 54, 66
Mott-Smith, 72
Muller, 19, 22
Multiple factors, 25, 82, 94, 102
Mutation, 2, 21-2, 58, 69-73
in nature, 47
rate, 21-2, 46, 69-70, 79
recessive, 22, 47, 61, 60-1
revive, 23, 67-8
sonic, 21, 68
Nileson-Fehr, 33
Non-adaptive characters, 77-8, 80
Nucleus, 2, 63-7
Lytechinus, 66
L. Nolte, 4
P. Painter, 19
Dunaria demissula, 90, 97-9
P. polytes, 36, 72
P. polytes, 36, 72
Partiolute inheritance, vii, 1, 34, 67
Patterson, 58
Peppered Moth, see Diston betularia
Phenotype, 28
Plastid inheritance, 64
Plough, 10
Poligeories, 82, 94, 102
Polymerorphism, 72, 74, 94-106
Balanced, 94-102, 106
Transact, 94, 102-106
Polyplody, 23-4, 90-9
Populations, estimates of, 77, 86-7, 89
large, 82-4, 86-7, 89
small, 82-3, 85-9
Poultry, 60
Andalusian, 59
comb-shape, 34-5, 60
Jungle fowl, 69
Leghorn, 60
Primus, 24, 65
Prophase, 15
Punnett, 34
Puro-lines, 69-70
Flyna, 101
Quad, 47
 Rabbits, 32-4
Raven, 77-8
Radium, 22
Range, Edge of, 91-3, 107
Recessive, 4
Roberts, 101
Robins, 104
Rodents, 64
Russell, 19, 64
Scarlet Tiger, see Panaxi4
Scully, 34
Scully, 85-90
Segregation, 1, 3-7, 25
Sex-controlled genes, 36
Sex-determination, 14
Sex-linkage, 14-16
Sex-linked genes, 14-16, 25, 36
Sheppard, vili, 90, 90-9
Skiel, 68, 98-7
Spartina alterniflora, 92-3
S. australis, 92-3
S. Townsendii, 92-3
Species, 77-8
origin of, 24, 92-3
Specific modifiers, 25-6, 49-50,
Stevens, 65
Sten, 19, 58
Struthers, 191
Sturnus vulgaris, 47, 54
Super-genes, 25-6, 95
Sutton, 2
Test, 85-90
Temperature, 29-34, 52
Timmer-Reevesky, 39, 87-8
Translocation, 23, 95
Valeriana officinalis, 93
Variability, extinction of, 68-9
Vegetative propagation, 91
Viability, 37-9, 103
Wheat, 74
Wright, 55, 84
X-chromosome, 14-16
X-rays, 22-3, 38
Y-chromosome, 14-16, 47, 54
MENDELISM AND EVOLUTION

The eighth edition of this classic work has been extensively revised to bring it in line with modern advances in evolutionary genetics. The book serves as a brilliant introduction to some aspects of this subject. Though primarily written for serious students, it has an introduction in which the principles of particular inheritance are briefly restated. It may thus be read by all those interested in evolution, whether they have made a previous study of genetics or not.


The general aim of the series is to offer students established books at prices they can afford. Titles will be drawn from all branches of science and technology.
MENDELISM AND EVOLUTION

The eighth edition of this classic work has been extensively revised to bring it in line with modern advances in evolutionary genetics. The book serves as a brilliant introduction to some aspects of this subject. Though primarily written for serious students, it has an introduction in which the principles of particulate inheritance are briefly restated. It may thus be read by all those interested in evolution, whether they have made a previous study of genetics or not.


The general aim of the series is to offer students established books at prices they can afford. Titles will be drawn from all branches of science and technology.

A SELECTION OF SCIENCE PAPERBACKS

SP1 Social Behaviour in Animals
SP2 Elements of Structural Geology
SP3 Atomic Structure and Chemical Bonding
SP4 Biological Laboratory Data
SP5 Semiconductors
SP6 Mendelism and Evolution
SP7 An Introduction to Electronic Analogue Computers
SP8 Classical Mechanics
SP9 Animal Ecology
SP10 Design for a Brain
SP11 Vision in Vertebrates
SP12 Bartlow’s Tables
SP13 The Plastic Methods of Structural Analysis
SP14 Mathematical Theory of Linear Systems

The price of 80p. applies to all books in this series. N. only.