

# **Blood relations**

## **BLOOD GROUPS AND ANTHROPOLOGY**

**A. E. Mourant**

---

# Blood relations

---

BLOOD GROUPS AND  
ANTHROPOLOGY

A. E. Mourant

MA, D. Phil., DM, FRCP, FRC. Path., FRS  
*Formerly Director, Serological  
Population Genetics Laboratory,  
St Bartholomew's Hospital, London*

OXFORD UNIVERSITY PRESS

1983

*Oxford University Press, Walton Street, Oxford OX2 6DP  
London Glasgow New York Toronto  
Delhi Bombay Calcutta Madras Karachi  
Kuala Lumpur Singapore Hong Kong Tokyo  
Nairobi Dar es Salaam Cape Town  
Melbourne Auckland  
and associate companies in  
Beirut Berlin Ibadan Mexico City*

© A. E. Mourant, 1983

*Published in the United States by  
Oxford University Press, New York*

*All rights reserved. No part of this publication may be reproduced,  
stored in a retrieval system, or transmitted, in any form or by any means,  
electronic, mechanical, photocopying, recording, or otherwise, without  
the prior permission of Oxford University Press*

*British Library Cataloguing in Publication Data*

*Mourant, A. E.*

*Blood relations.*

*1. Blood groups*

*I Title*

*612'.11825      QP98*

*ISBN 0-19-857580-7*

*Printed in Great Britain by  
The Thetford Press Limited, Thetford, Norfolk*

---

## Preface

---

Until the time of the Second World War, physical anthropology meant the comparative study of the anatomical characteristics of the body in different human populations and individuals. It signified particularly the measurement of the body and its parts, especially the skull, in living and dead persons.

Since then, however, arising largely from the intensive development of blood transfusion promoted by the war, the blood groups, supplemented more recently by other hereditary biochemical characteristics, have come to provide an alternative means of classification of the living which has to a great extent replaced direct body observations.

As a scientific tool, the blood groups, with their precisely understood genetics, are probably easier to use than physical measurements, but the reasons behind their application are far less obvious to the layman.

The objects of this book are to explain, in as simple terms as possible, how blood-group anthropology works and how it is applied to particular populations, and to set out some of the conclusions that can be drawn from it as to relations between populations.

In a final chapter the wider implications of the subject are examined, such as relations between genetic characteristics, susceptibility to particular diseases, and exposure to various environmental factors.

Every effort has been made to ensure that the statements and conclusions of this book are as accurate as possible. Readers are assured that this will not later have anything to unlearn, but they are not asked to take this on trust. A full bibliography would run to many thousand references, but a short select bibliography has been included. Its primary purpose is to serve as a reading list, though occasional references are made to it in the text. Readers who wish for fuller documentation should consult the author's books, *The distribution of the human blood groups*, *Blood groups and diseases*, and *The genetics of the Jews*, listed in that bibliography.

The present book is based, to a considerable extent, upon the works just mentioned, written in collaboration with Dr Ada C. Kopeć and Mrs Kazimiera Domaniewska-Sobczak, to whom I express my warmest thanks. They are, of course, in no way responsible for the present work. I am most grateful also to Mr G. Misson and Professor D. F. Roberts, and to the Staff of the Oxford University Press, for reading the whole text and

## vi Preface

making constructive suggestions, most of which I have adopted. I am also deeply grateful to my wife for typing several drafts of the book from my untidy manuscripts. I am indebted to Mrs. Marie Crookston for suggesting the title of the book.

*Jersey*  
March, 1962

A. E. M.

---

## Contents

---

1. How we recognize people	1
2. Elementary genetics	4
3. Africa	36
4. Asia	59
5. Europe	73
6. The Jews and the Gypsies	90
7. The Pacific islanders	99
8. Amerindians and Eskimos	108
9. Causes of gene frequency change	115
Further reading	131
Index	141

---

# I. How we recognize people

---

## Inherited and acquired characteristics

One of the most important faculties of human beings, as indeed of all 'higher' animals, is that of recognizing individual members of their own species. It is a faculty which we all take very much for granted, and if one of us were unexpectedly asked how we did it, even the immediate and perhaps superficial answer would require some moments' thought.

Facial conformation is, of course, all important, yet notoriously difficult to describe, especially when it is a matter of distinguishing between two or more members of one's own population or between persons of the same 'race'. One reason for this is that the mind, in interpreting the results of visual observation, pays considerable attention to 'expression' which consists of subtle indications of the emotions of the person observed, brought about by slight contractions of the facial muscles. We have all seen a person alter in appearance almost out of recognition by the sudden removal of some source of worry, such as an unhappy personal relationship, yet the main shape of the face, and certainly the shape of the bones which form its main structure, have changed not at all. It is for this reason that the interpretations of the sensitive painter convey much more to most of us than the scientific descriptions of the anthropologist.

Yet for scientific purposes we need to be able to describe the individual in unambiguous terms which will mean the same to all readers.

We have so far mentioned only the shape of the face, because it is at the same time the most important characteristic in everyday life, and also perhaps the most difficult to describe. But the shape and size of the body as a whole, and of its parts, are also of obvious descriptive importance. Colour of eyes and hair and, when we come to major 'racial' distinctions, colour of skin, are also of outstanding importance, as is the texture of the hair. These differences in colour and texture are much more easy to put into words than are subtle anatomical distinctions. The former, together with obvious 'racial' anatomical characteristics such as slanting eye openings and everted lips, form the basis in most people's minds of a separate set of distinctions of a quite different kind from those which we use in distinguishing individuals of our own race. Later on we shall consider the question of whether these really constitute two separate scientific levels of description and distinction.

The characteristics just described are mainly inborn and hereditary

## **2 How we recognize people**

rather than acquired, but some, especially body weight and the contours of the soft parts of the body, are mainly acquired, and more dependent upon the state of nutrition. Skull shape can be modified permanently by pressures applied during infancy.

To change from morphological and visual characteristics to auditory ones, language and accent are learned, but the characteristic sound of the voice, which is most important in personal recognition, while largely dependent upon the hereditary anatomy of the air passages, is perhaps to some extent learned from parents and teachers.

Gestures and other body movements, important for recognition at a distance or from behind, are mainly learned but certainly partly hereditary.

Body painting, hair dyeing and dressing, and clothing are of course entirely acquired, though artificial and innate colour may be difficult to distinguish from one another.

Body odour is mainly dependent upon diet and hygiene, but is almost certainly partly dependent upon the morphology and biochemistry of the skin glands.

It will be seen that we recognize people mainly by the shape and colour of the body and its parts. Most of the describable features are essentially hereditary in nature but they can be affected by the history of the individual both before and after birth. There is still much to be discovered as to the extent to which each one is determined by heredity on the one hand and by the environment on the other. Both influences are always at work upon these features and they may be difficult to disentangle; the study of their heredity belongs to the science of genetics: that of the effects of environment to ecology.

In the utilitarian business of recognizing individuals, it does not greatly matter whether what we observe is inherited or is acquired through the effects of the environment. If we are concerned about improving the environment then the acquired characteristics are primarily important, but if we want to study and distinguish individuals, the inherited ones are of major importance. This is especially the case if we want to be able to keep track of an individual over a long period of time, as for instance for police purposes. In this respect the importance of the fingerprint patterns, which are essentially hereditary, and which become fixed at an early period in antenatal life, has long been recognized.

### **Individuals and populations**

So far we have considered solely the identification of individuals, and indeed a study of humanity must always start with individuals. However, the anthropologist is interested more in populations than in individuals. He will be concerned with environmental influences, but primarily with hereditary ones. He will wish to identify the historical and hereditary

relations between populations, trying to answer such questions as whence, in Africa, the ancestors of present-day American Negroes came, or to what extent modern Jews are descended from the Palestinian Jews of Biblical times.

For such purposes characteristics are needed which are determined solely, or almost solely, by heredity and, as we shall see, it is a great advantage to make use of characteristics not merely solely determined by heredity, but also determined in a known way. Some of the characteristics so far mentioned appear to be shaped solely by heredity but for none of these directly observable features is the precise mechanism of inheritance known.

### **Visible and invisible characteristics**

In contrast to these visible characteristics, research during the present century shows that there is a class of invisible ones, fixed by heredity in a known way at the moment of conception, immutable during the life of the individual, and observable by relatively simple scientific tests.

These are the 'blood groups', to which have been added in recent years a large number of other chemical features of the blood. The longest known and most widely used of these sets of characteristics, recognized 80 years ago, is the system of ABO blood groups, A, B, AB, and O, to one of which all human being belong, and which are familiar to all donors of blood for transfusion. And discovered, it seems, almost yesterday are the HLA or histocompatibility groups, detected by blood tests but used to ascertain compatibility in the case of proposed grafts of kidneys and other organs.

These characteristics belong to a number of genetic systems, a term defined in the next chapter, and those of any one system are inherited independently of those of all other systems. Since between fifty and one hundred such systems are now used in routine tests, the numbers of possible combinations are of astronomical dimensions and, for police purposes as an example, we are now approaching the situation where, except for identical twins, every human being will be distinguishable from every other one.

For describing and classifying populations, too, these blood characteristics have now long surpassed, and indeed largely superseded, studies of anatomical features in their usefulness to anthropologists.



---

## 2. Elementary genetics

---

Before we can use, or understand the use of, any inherited characteristics in the study of individuals and populations, we must know how these characteristics are inherited.

Rather surprisingly, the mechanisms of biological inheritance are essentially the same throughout the whole living world. The basic principles were discovered in the 1850s by an Augustinian monk, Gregor Mendel, growing peas in a monastery garden at Brünn or Brno in what is now Czechoslovakia. He made and published his discoveries at about the same time as Darwin published *The origin of species* but, whereas Darwin's work gave him immediate fame, that of Mendel was almost entirely ignored or forgotten until the principles were independently rediscovered about 1900, the year in which the blood groups also were discovered.

### Cells and reproduction

The science of genetics is largely concerned with the inheritance of specific characteristics, such as those of shape, colour, and biochemistry. Before we look at such matters, however, we need to know the main anatomical and microscopic facts associated with the transmission of life from one generation to the next. Many forms of life consist of single separate microscopic cells, which in most cases reproduce by a process of splitting into two. Most organisms, however, both animals and plants, that are big enough to be seen by the unaided eye, consist of thousands, and in most cases millions, of microscopic cells, and reproduce by a sexual process. This involves the production by the parents of specialized reproductive cells. Two cells, one from each parent, come together and unite to form a single new cell which grows, divides into two, and continues to grow and subdivide to give rise to a new multicellular individual. The female or egg cell, known as the ovule in plants or the ovum (plural, ova) in animals, is relatively large for a cell, and contains, besides the purely reproductive part, a supply of food for the new organism.

The male reproductive cell is smaller than the female. In higher plants it is produced by the pollen grain during a somewhat complicated process which takes place within the flower. In animals the microscopic spermatozoon (plural, spermatozoa) is motile and swims to seek out and unite with the ovum. In fishes and amphibians ova and spermatozoa are in most cases shed into water and there unite. In reptiles, birds, and mammals

including man, a fluid containing the spermatozoa is introduced by the male into the reproductive passages of the female.

Long before the mode of inheritance of individual characteristics was understood by anyone except Mendel, many of the microscopic details of the process of union had been worked out and were ready for incorporation into the science of genetics when the scientific world itself was ready. Every somatic (body) cell, and every reproductive cell, male or female, plant or animal, consists of a semi-fluid cytoplasm surrounding a denser nucleus. The nucleus can readily be made visible under the microscope by staining with certain dyes and, under higher powers of the instrument, made to show the details of its structure and the changes which these undergo during the reproductive process.

At a relatively low magnification the nuclei of the male and female reproductive cells are seen to unite into a single nucleus within what is, for the moment, a single cell. The new nucleus, and the cell of which it forms a part, now divides into two; each of the halves again divides, and the process is repeated almost indefinitely. In the nineteenth century all that could be seen were dead preparations representing stages in the process, but the whole process can now be watched directly and photographed by micro-cinematography.

### Chromosomes

Under high magnification the nucleus is seen to contain a number of threads known as chromosomes, which are constant in number in any one species of animal or plant. The number in each of the reproductive cells, male or female, is half that in each of the body cells. The reproductive cells are said to be haploid (from a Greek word meaning single) while the body cells are said to be diploid (meaning double).

At each process of union of two reproductive cells, each such cell or gamete, one from the male and one from the female parent, contributes half the chromosomes of the new single cell, or zygote. When the zygote divides and subdivides, as described above, each resulting cell contains the full or diploid number of chromosomes. In this case too only dead 'stills' could at first be examined, but it has now become possible to see and photograph the whole active process.

In spite of general ignorance of the 'laws' governing the inheritance of body characteristics in general, it was realized before the end of the nineteenth century that the chromosomes were in some sense the carriers of such inheritance.

This development was largely due to August Weismann, a German zoologist who has never received the full recognition which the scientific world owes him for his interpretation of the facts of heredity and cytology (the science of cells). Unlike Darwin and Mendel, who made very great

## 6 Elementary genetics

single discoveries but had, as we should now say, 'one-track minds', he was a man of very wide knowledge, a 'scientists' scientist' who, as Cyril Darlington put it, was able to interpret evolution to the cytologist, and chromosomes to the evolutionist.

### Mendel and the mechanism of heredity

The essence of Mendel's approach to heredity was that he recorded everything in numbers, and at every stage kept the progeny of every plant, and every seed of every plant, separate. To understand his work on the common pea we must realize that the coating of a plant seed is part of, and partakes of the genetic nature of, the parent plant. But the seed itself is a complete embryo plant of the next generation, arrested temporarily at an early stage of development.

Darwin never seems to have heard of Mendel or his work. Mendel, however, though he began his work before Darwin published *The origin of species*, became in due course fully familiar with this book. Unlike Darwin, however, he was also familiar with the cell theory of reproduction and development. He knew that single pollen grains fertilized single ovules, but he took the precaution of confirming this by experiment.

He found that the pea plant was fully capable of fertilizing its ovules with its own pollen. He established a number of lines of plants each of which was 'pure' for a particular characteristic such as tallness, shortness, pink or white flowers, as defined by the fact that after many generations of self-fertilization no change in this characteristic ever appeared in the progeny.

He then tried crossing pure lines. For instance, he crossed tall and short plants, using both pollen of tall plants on ovules of short plants, and vice versa. In each case all the progeny in the first generation were tall. He then grew a large number of the seeds of these plants, and in the resulting plants there was a constant ratio of almost exactly three tall to one short. He allowed the flowers of each of these plants to fertilize themselves, and then came the crucial observation. The self-fertilized seeds of the short plants produced nothing but shorts, which bred true in subsequent generations. Of the tall plants approximately one in three gave nothing but tall offspring, which continued to breed true in all subsequent generations. The other tall ones behaved exactly like their parents, giving approximately three tall to one short offspring.

The results in the first generation are explained by the statement that in peas tallness is 'dominant' to shortness (in man, however, stature is of highly complex heredity). In terms of what we should now call genes, each of the cells of the original tall plants carried two genes for tallness, symbolized by *T*. Those of the short plants carried two genes for shortness, symbolized by *t*. Thus all the body cells of the pure tall plants had

the combination  $TT$  and all their reproductive cells, whether male or female, carried a single  $T$ . Similarly all the body cells of the short plants had the combination  $tt$ , and all their reproductive cells carried a single  $t$ .

Thus all the hybrid plants must have the constitution  $Tt$  and all will be tall, since  $T$  is dominant in expression to  $t$  (or  $t$  is recessive to  $T$ ).

However, when we produce offspring from these hybrids by self-fertilization, each plant will produce equal numbers of  $T$  and  $t$  female reproductive cells, and equal numbers of male  $T$  and  $t$  reproductive cells.

A  $T$  female cell will have equal chances of being fertilized by a  $T$  or a  $t$  male cell, giving equal numbers of  $TT$  and  $Tt$  offspring, all of which will be tall. The  $t$  female reproductive cells will give rise to equal numbers of  $Tt$  (tall) and  $tt$  (short) plants. Thus the overall ratio will be 1  $TT$ : 2  $Tt$ : 1  $tt$  of which the  $TT$  will be true-breeding tall plants, the  $Tt$  tall but not true breeding, and the  $tt$  true-breeding short plants. We should now call the  $TT$  and the  $tt$  plants homozygous (adjective) or homozygotes (noun) while the  $Tt$  are heterozygous or heterozygotes. We shall see later that dominance and recessiveness are not universal characteristics of gene expression. There are many genetic systems in man where the heterozygotes can be distinguished by suitable tests from both the homozygous types.

The new and fundamental point about these observations is that, whatever may be their expression or failure of expression in individual plants, genes for tallness and shortness remain distinct in successive generations. Every time that reproductive cells are formed the genes *segregate* separately. Many, if not most, biologists had previously thought that there was a blending not only of the expression of what we should now call genes, but of the genes themselves. We shall deal at a later stage with the much more difficult problem of characteristics such as human stature, to show how family studies which might at first sight seem to imply a blending not only of effects but of genes, are probably explicable in terms of Mendelian segregation.

So far we have used the word 'characteristics' for the separate hereditary properties of plants and animals. Now however that we have moved into the field of precise genetics we shall use the technical word 'characters' in this sense.

Mendel went on to study a further six pairs of contrasting characters in the pea, and in each case he found segregation, with the same ratios of types as he had observed for tallness and shortness.

He then embarked on a study of the effects of combining two pairs of characters in a single experiment, for instance tallness (dominant) and shortness (recessive) combined with colour of flowers (dominant) and whiteness (recessive). When a tall plant with coloured flowers was crossed with a short one with white flowers, the first generation hybrids were all tall and coloured. However, when these were allowed to self-fertilize, and the seeds grown, the next generation consisted of tall coloured, tall

## 8 Elementary genetics

white, short coloured, and short white. When enough of these had been grown to eliminate chance effects, the ratios found were very close to  $9 : 3 : 3 : 1$ , these being the only ratios which would separately yield the ratio  $3 : 1$  for each pair of characters taken separately. Thus not only did the genes for two contrasting characters segregate separately from one another, but they also segregated separately from those for other pairs. As Mendel pointed out, the principle could be extended indefinitely to combinations of three or more pairs of characters.

The establishment of the separate segregation of pairs of alternative characters was an essential step in the working out of the 'laws' of genetics, but there are exceptions to this rule, and Mendel was in a sense fortunate that he did not come across one of these in his basic researches, though their recognition and explanation early in the next century were necessary for the further advance of the science.

### The rediscovery of genetics

The forgotten work of Mendel was rediscovered independently in 1899 and 1900 by three investigators, Tschermak, Correns, and De Vries. This rediscovery initiated a period of intensive investigation, which still continues, involving integrated studies of experimental breeding of plants and animals, microscopic examination of cells and chromosomes, and ultimately biochemistry of the most advanced nature. We shall not attempt to describe these developments, except as they are illustrated by the genetics of the blood groups and other characters used in anthropology.

The main 'work-horse' of the next generation of geneticists was the fruit fly, *Drosophila melanogaster*. It was the organism chiefly used in working out the relation between chromosome morphology and gene behaviour, initially by H. J. Muller, and then by hundreds of other workers. It has a short generation time of ten days, it is very cheap to feed and maintain, it has hundreds of easily recognizable simply inherited characters, and it has four pairs of readily visible and distinguishable chromosomes.

This and many other small animals, as well as numerous plants, have been used in working out the fundamentals of genetics. Few doubted that the same principles would prove to apply to heredity in man or *Homo sapiens*, but the human species has, for this purpose, the disadvantages of a long generation time, and of not being available for experimental matings. However, in the long run these principles have been worked out for man, who has indeed become an important organism in the more recent elucidation of the principles of biochemical genetics. It must however be understood in what follows that in such matters as the correlation of heredity of particular characters with chromosome behaviour, the

principles were already fully known before it became possible to apply them to man.

### Landsteiner and the ABO blood groups

In 1900, the year which saw the rediscovery of Mendel's principles, two events took place which at first sight bore no relation to genetics. Landsteiner in Austria discovered the human ABO blood groups, and Ehrlich and Morgenroth in Germany discovered similar phenomena in goats. The impetus came not from genetics or from human biology but from the techniques of bacteriology and the phenomena of immunity to bacteria; when animals or human beings have been infected, naturally or experimentally, with certain bacteria, their blood acquires the property of agglutinating preparations of the same bacteria; when serum from such blood is added to a uniform suspension of microscopic bacteria, they agglutinate or come together in clearly visible clumps.

Blood is, of course, a suspension of microscopic red and white 'corpuscles' in a fluid. The more numerous red corpuscles are in fact cells which have lost their nuclei; they are nevertheless often referred to as 'red cells'. They consist of a membrane enclosing a solution of the red protein haemoglobin, which in the process of the circulation of the blood serves to carry oxygen from the lungs to the tissues.

The white corpuscles, only about one-thousandth as numerous, are true cells with a nucleus and cytoplasm. We shall for the moment be concerned solely with the red cells but shall return to the white cells later. The almost colourless fluid part of the circulating blood is known as 'plasma'. It contains substances which cause the blood to clot upon shedding. When the clot has separated from the shed blood the remaining fluid, differing from plasma only in the absence of the clotting principles, is known as 'serum'. Landsteiner found that, when suspensions of red cells in weak salt solution ('saline') from a number of individuals are tested separately by the addition of serum from other individuals, agglutination of the red cells takes place in some but not in other cases. Landsteiner actually distinguished three types to which a fourth was very soon added. It is not quite clear to whom should be given the credit for finding this fourth type. The four types are now named A, B, AB, and O, the symbol O indicating the absence, on the surface of the red cells, of any of the blood group substances. The symbol A indicates the presence of a substance A on cells, B the presence of a substance B, and AB the presence of both substances. We shall consider later the precise nature and origin of these 'substances'. For the present purpose they are to be regarded as 'antigens' analogous to characteristic antigens present on the surface of bacteria. It is a property of antigens that they combine with specific antibodies present in sera, the combination being demonstrated by a visible

## 10 Elementary genetics

phenomenon such as agglutination. An antibody is named after the antigen with which it combines, preceded by the prefix 'anti-', the serum of a group A person contains the antibody anti-B; that of a group B person contains anti-A. Serum of a group O person contains both anti-A and anti-B, and that of a group AB person, neither. Thus the serum of any person contains as many kinds of antibodies as it can, subject to the limitation that the serum must not cause the agglutination of the subject's own red cells.

This rather complex situation is summarized in Table 1. The reader should not be discouraged by a difficulty in remembering the meaning of the new words just introduced. I well remember my own difficulty in remembering the distinction between antigens and antibodies. It is useful, as a mnemonic, to remember that antigens *generate* antibodies.

TABLE 1  
*The ABO blood groups: antigens and antibodies*

Blood group	Blood group substances (antigens) in red cells	Antibodies present in plasma (or serum)
O	none	anti-A, anti-B
A	A	anti-B
B	B	anti-A
AB	A and B	none

The new discovery was presumably recognized at the outset as demonstrating a set of more or less permanent characteristics of individual human beings. The blood groups were not at first seen as having any medical consequences, nor were they recognized as hereditary. Within a few years, however, they were shown to be indispensable indicators of compatibility between donors and recipients of blood given in transfusion. Blood transfusions had been attempted on many occasions during the previous two hundred years in the treatment of haemorrhage or anaemia, sometimes with success, but often followed by rather sudden and unexplained death, now recognized as being due to incompatibility. By this one discovery transfusion was rendered almost completely safe.

### Animal blood groups

We must now go back to another discovery made in the momentous year 1900, that of blood groups in goats. The investigators were Ehrlich and Morgenroth. The former is better known for his discovery of salvarsan, the precursor of all the antibiotics, and the first chemical substance able to kill an infective microorganism (in this case that of syphilis) without

seriously endangering the patient. Older readers may remember a splendid documentary film, *Dr Ehrlich's magic bullets*.

The goat blood groups must have appeared even more useless than those of man, and I do not know whether veterinarians have ever applied them in transfusing goats. However, the paper describing them came to the notice of a newly qualified Polish doctor, Ludwik Hirszfeld, living in Germany. He was about to embark on a career of research, and decided to search for blood groups in dogs. Having succeeded in this, and never having heard of Landsteiner's work, he had decided to look for blood groups in man. It was at this point that he first read Landsteiner's classic paper which, far from discouraging him, only reinforced his decision to work in this field. Shortly afterwards he was thrilled to meet the great man. But he himself was destined for a career in blood group research of comparable distinction to that of his predecessor.

### The heredity of the blood groups

In 1910, jointly with his Professor, Baron von Dungern, Hirszfeld showed that the blood groups were inherited as Mendelian characters. Apart from a few rare diseases these were almost the first characters shown to be inherited in this way in man. It was at this time thought that genes could exist only as sets of two (not more) alternative or allelomorphic genes (like tallness and shortness in Mendel's peas) and the results were therefore interpreted in terms of two such pairs: *A* and absence of *A*; *B* and absence of *B*; and these were thought to combine in the manner already described for tallness and shortness with colour and whiteness in peas. It was soon shown for other organisms that there could indeed be sets of three or even many more allelomorphs, but it was not until 1924 that Bernstein gave the correct explanation, which is that the blood groups are determined by a set of three allelomorphic genes, *A*, *B*, and *O* (of which any one individual carries only two). Genes *A* and *B* each express themselves dominantly with respect to the *O* gene, but *A* and *B* are not dominant with respect to one another—in the heterozygote with both

TABLE 2  
*Genotypes of the ABO blood groups*

Genotype	Blood group
OO	O
AO	A
AA	
BO	B
BB	
AB	AB



## 12 Elementary genetics

*A* and *B* genes *both* substances A and B are present on the red cell. These relations are summarized in Table 2.

### Genes and chromosomes

Very early in the twentieth century the microscopically visible chromosomes were clearly shown to be threads upon which the genes had specific places. This was most fully demonstrated in the case of the fruit fly, *Drosophila melanogaster*, which has only four pairs of chromosomes. Since each member of the half set of chromosomes present in the reproductive cell enters separately into the fertilization process we now have a clear mechanical picture of why sets of genes on different chromosomes should segregate separately, as Mendel showed them to do. But it was soon found that certain pairs of genes did not segregate independently of certain other pairs, and this was then correlated with the fact that they were situated on the same chromosome, or rather, on a chromosome of the same pair.

Taking as an example another species of pea, the sweet pea, *Lathyrus odoratus*, Punnett has shown that purple colour is dominant to red, and long pollen grains to round ones (the pollen shape is a character of the parent plant). Each pair of characters taken by itself behaves exactly as Mendelian principles would indicate. Moreover, if we hybridize purple-long with red-round, we get in the first generation nothing but the double dominant type, purple-long. However, the next generation, where simple Mendelian principles would have predicted a ratio 9 : 3 : 3 : 1 between the types, we find a ratio between purple-long : purple-round : red-long : red-round very close to 7 : 1 : 1 : 7, i.e. a great excess of the original types. There is said to be linkage between the two systems of allelomorphs, and this we now know to be due to the *loci* (plural word of which the singular is *locus*—Latin for place) being on the same pair of chromosomes.

If however the chromosomes reproduced in every generation as single entities we should expect *all* the members of this generation, not merely seven-eighths of them, to be of the two original types. Thus, in the formation of the chromosomes of the reproductive cells there has been a certain amount of interchange of genes, a process known as crossing-over, and one which has now very often been observed under the microscope.

The genetics of man tended until about 1950 to lag far behind that of other organisms. This applied particularly to the study of linkage and even more so to the microscopic study of the chromosomes, which presents particular technical difficulties, so that the examination of the chromosomes of the onion had become a regular student exercise long before the human chromosomes were even precisely counted. We shall